Experimental Incubation of Chum Salmon *(Oncorhynchus keta)* in a Japanese-Style Hatchery System

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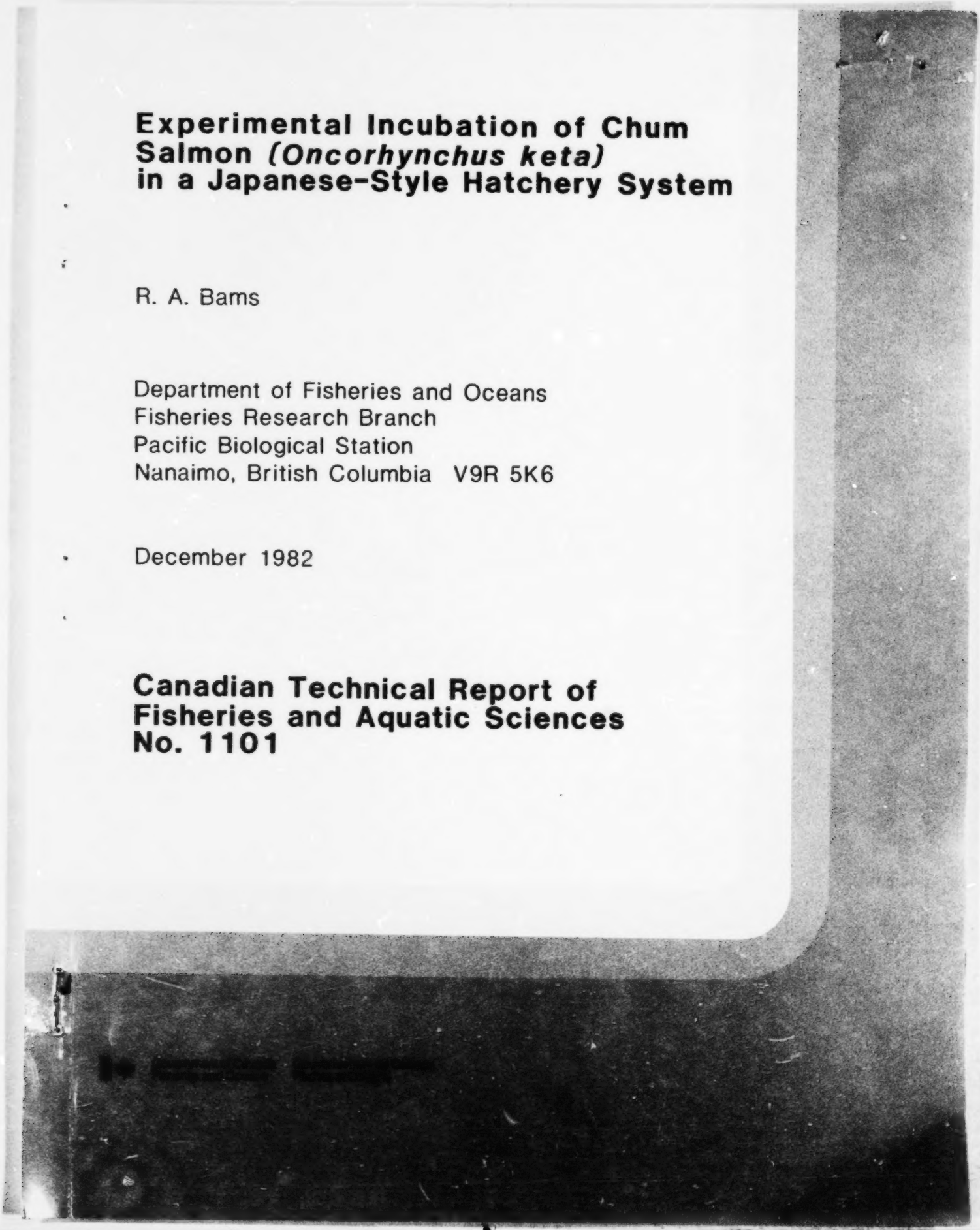

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EXPERIMENTAL INCUBATION OF CHUM SALMON (*Oncorhynchus keta*) IN A JAPANESE-STYLE HATCHERY SYSTEM

by

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ABSTRACT

R. A. Bams. 1982. Experimental incubation of chum salmon (Oncorhynchus keta) in a Japanese-style hatchery system. Can. Tech. Rep. Fish. Aquat. Sci. 1101: viii + 65 p.

Performance of an experimental Japanese-style chum hatchery (channel) was evaluated at different levels of fish density, water flow, and gravel depth, and compared with that of a control treatment, deep-gravel incubators (box). Ambient levels of dissolved oxygen, ammonia, nitrite, pH, and temperature were measured. Only oxygen dropped below normally acceptable levels in some cases. Several biological responses were evaluated. Survival from hatching to emergence was 95% or better in all cases but one, and that case could easily be rectified. Time of emergence was marginally affected by density and flow, but slowed considerably with increasing gravel depth and with increasing distance along the channel (i.e. with increasing cumulative density). Box fry emerged latest. Length at emergence was generally promoted by increased flow, and by greater gravel depth when flows were sufficiently high. Largest average sizes were achieved in the gravel boxes. Stage of development at emergence was less advanced in the channel fry than in the box fry, by the equivalent of about 7 days' growth. Stage of maturity was positively correlated with depth of gravel. Yolk-conversion efficiency was highest in the gravel boxes and decreased generally with decreasing gravel depth and increasing flow. Responses were quite complex generally, due to interaction among factors and, it is suggested, variable alevin and fry behavior.

Key words: gravel incubation, keeper channel, chum alevins and fry, evaluation.

RÉSUMÉ

R. A. Bams. 1982. Experimental incubation of chum salmon (Oncorhynchus keta) in a Japanese-style hatchery system. Can. Tech. Rep. Fish. Aquat. Sci. 1101: viii + 65 p.

On a évalué le rendement d'une piscifacture expérimentale de style japonais (canal d'élevage) pour l'élevage du saumon kéta en variant la densité des poissons, le débit d'eau et la profondeur du gravier. Ce rendement a par la suite été comparé à celui des incubateurs à gravier profond, la méthode-témoin. On a mesuré les taux ambiants d'oxygène dissous, d'ammoniaque, de nitrite, ainsi que le pH et la température. Seuls les taux d'oxygène ont, dans quelques cas, baissé au-dessous des niveaux normalement acceptables. On a aussi évalué plusieurs réponses biologiques. La survie de l'éclosion à l'émerence s'élève à 95 % ou plus dans tous les cas sauf un; celui-ci peut facilement être rectifié. La densité et le débit one eu un effet marginal sur moment de l'émergence, lequel a ralenti considérablement par rapport à la profondeur croissante du gravier et à la distance le long du canal (c.-à-d. par rapport à la densité cumulative croissante). Les alevins en incubateur sont apparus le plus tard. La longueur à l'émergence a été généralement favorisée par un débit plus volumineux et par une couche plus profonde de gravier quand les débits étaient assez élevés. Les plus grandes tailles moyennes ont été obtenues dans les bacs à gravier. Le stade de développement à l'émergence était moins avancé chez les alevins élevés dans les canaux que chez ceuz élevés en incubateurs, une différence équivalente à environ sept jours de croissance. Le stade de maturité est en corrélation positive avec la profondeur de gravier. L'efficacité de conversion de la vésicule était plus élevée chez les alevins élevés en incubateurs et diminuait en fonction d'une diminution de la profondeur du gravier et d'ine augmentation du débit. En général, les réponses ont été très complexes vu l'interaction entre les facteurs ou peut-être le comportement variable des alevins vésiculés et des alevins à vésicule résorbée.

Mots-clés: incubation sur gravier, canal d'alevinage, alevins vésiculés et alevins à vésicule résorbée de saumon kéta, évaluation

INTRODUCTION

With the advent of Japanese-style chum hatcheries in British Columbia (cf. Bailey 1979), there was a need to develop an appreciation for the sensitivity of such systems to variations in some of the prescribed parameters. Considerable variation exists among Japanese installations (e.g. Helle 1979; Moberly and Lium 1977), presumably in response to local discrepancies in environmental or fish characteristics, or simply reflecting allowable leeway in design characteristics. Further, the system may have different requirements for optimal performance under B.C. conditions and with B.C., as yet exclusively uncultured, stocks. This report covers an experiment designed to evaluate the effects of different flow rates, loading densities, and gravel depths, within the confines of a Japanese-style system, on some in-situ conditions and biological responses of the brood.

A small Japanese-style hatchery was available, which had been built at an existing fish-cultural facility for a series of evaluation tests. It was modified to contain 24 experimental units to accommodate a factorial type design. A "control" population was created by raising an additional group of chum fry in proven design, deep-substrate gravel incubators, known to produce fish comparable to naturally incubated stock (Bams 1974).

Biological responses were evaluated by the author and included survival (to the egg and fry stages only), length, weight, stage of development, time of emergence, and efficiency of yolk conversion. Environmental factors, comprising pH, temperature, dissolved oxygen, ammonia, and nitrite, were measured concurrently by C. Lam of this institution. Growth was studied for 8 wk following emergence, but that study will be published separately.

MATERIALS AND METHODS

Two concrete Japanese-style incubation ("keeper") channels were constructed in 1976 at the Departmental fish-cultural facility at Rosewall Creek, 80 km north of Nanaimo, on the east coast of Vancouver Island, British Columbia, for a series of tests completed in spring 1979. The channels are outdoors, lie side by side, have independent water supplies and outlets, and each can be covered with a set of rough cedar planks. Dimensions and modus operandi conform closely to the usual Japanese installations (Moberly and Lium, 1977). Each channel measures 12.5 m long, by 1.8 m wide, by 18 cm deep and was divided in two lengthwise with a central 14 by 14 cm (inside) open trough constructed of wood. Each half was then divided into 6 successive experimental units, each 1.4 m long by 0.8 m wide with a net surface area of 1.10 m^2 (11.8 ft^2). Units were separated with vertical stainless steel screens, having 8 meshes to the inch (approximately 3.2 mm) and 0.025 in (0.6 mm) dia. wire for a 0.64 open construction.

Each unit was equipped with two separate outlets, one for water sampling and one for egress of the fry following swim-up. The water samplers were weighted plastic tubes of 6.3 mm dia., perforated with 1 mm dia. holes, situated at the downstream end on the bottom in the gravel layer or above the surface of the gravel, across the full width of the unit. Each sampler was connected to a 6.3 mm dia. plastic hose running down the central trough to the outside. Each hose was individually marked and, by means of a quick connector, could be connected to a peristaltic pump to obtain the samples. Initially, the perforations in the sampling tubes were too few to allow a reasonable sampling rate and alevins would be sucked into them and plug the holes. The samplers were modified by installing sleeves of 19.1 mm dia. stiff plastic hose over them. The two open ends were sealed and the bottom half punctured with numerous 1 mm perforations. The modified versions performed well.

Measurements were made weekly. Oxygen was measured by the unmodified Winkler method. Ammonia was measured by the indo-phenol blue method, and nitrite by the pink azo-dye method. A Corning pH-meter, model 125, was used with a Fisher glass electrode and a calomel reference. Details of methodology followed Stainton et al., 1977.

The fry outlet from each unit was a 1/2 in (13 mm) inside dia. PVC elbow mounted through the wall of the central trough, at about 10 cm above the floor and 4 cm ahead of the downstream screen. Each one was connected to a length of 1/2 in (13 mm) inside dia. PVC thin-wall tubing extending the length of the channel through the central duct. All tubes continued an additional 17 m to a sampling location, where the outlets of the pipes were some 60 cm below the level of the channels. The tubes discharged into separate marquisette netting collecting baskets, each about 25 cm square and suspended side by side to a depth of about 20 cm in a level-controlled trough, which contained the joint outflow water. The tubes were kept empty and closed off with a cork on the channel side until swim-up was observed. Once started the tubes acted as siphons and maintained flows without developing air locks. Raising or lowering the outlets of the tubes along a wooden riser attached to the collecting troughs effectively controlled water flows. The tubes ran at 1 Lpm each initially, but this was soon increased to 2 Lpm each to increase the rate of fry egress.

Flows to the channels were maintained at 40 and 80 Lpm during most of the incubation period. Flow rates were measured at regular intervals at the downstream level control weir. A stopwatch was used in combination with a box of known volume designed to catch the entire section's flow. Flows varied little, with one exception on March 28 when a high wind knocked over the observation shed and blew it against the control valves of the high flow channel, no more than doubling the flow for about one hour. During the final 2 weeks of the operation flows were arbitrarily increased in channels and siphon tubes to facilitate outmigration of the remaining fry.

Under normal conditions of flow, water depth in all channels averaged 15 cm, which, at 40 and 80 Lpm and ignoring the presence of any gravel, gave average linear velocities of 33 and 66 cm/min respectively. Water entered from separately valved PVC manifolds at the top end of each channel. Flows stabilized over a distance of 6.2 m before entering the first unit. Water depth was controlled by an outlet weir situated 0.9 m below the

ultimate unit in each channel. When fry migration began, flows were increased to all channels to compensate partially for the draw-off by the siphons. The increase was about 30% to the low flow and 15% to the high flow channels. Flow rates, at least in the more distal units, were still affected, but over the entire incubation period the differences are unlikely to have been of any consequence and are ignored.

Experimental "controls" were eggs from the same source, incubated at comparable densities and flow rates in 4 scaled down deep-substrate incubators. These incubators measured approximately 0.3 x 0.6 x 1.2 m deep and were in all respects other than area identical to the usual deep-gravel box, as described in Bams and Crabtree, 1974. They were loaded with 16,000 or 32,000 eggs each at closely maintained upwelling flow rates of 8 and 16 Lpm respectively. Water supply and temperature regime were the same as that of the channels. Fry emerged by migrating to the surface, whence the water flow carried them through the outlet into a screened collecting bucket.

The parent fish were Big Qualicum chums, spawned artificially on Dec. 3, 1979. We used the eggs of 248 females, average egg content 3,094, and the sperm of 149 males. Eggs of 10 females were collected at a time and fertilized with the milt of 6 males in a 5 imp gal (23 L) bucket. They were washed, water-hardened for not less than 1 h, and transported in these buckets to Rosewall Creek, 18 km by road. Upon arrival, eggs were mixed together in groups of 3 buckets at a time in a 45 imp gal drum. They were treated with Wescodyne at 100 ppm for 10 min, and placed, approx. 24,000 at a time, in special incubators. These were single-pass, 4.5 Lpm, upwelling incubators, 30 cm in diameter and 20 cm deep. Eggs were treated weekly with malachite green at 5% for 1 h. When eyed, dead eggs were removed and remaining eggs were counted electronically and divided randomly into the 28 required experimental groups.

Shortly before hatching, at about 428 C-degree days, eggs were transferred to the channels, and spread evenly on hatching screens. These screens were made of Vexar with 6 mm holes, approximately 0.88 m^2 in area, and installed horizontally, 7 to 8 cm above the floor. At the highest density, eggs were 3 to 4 layers deep on the screen. Egg diameter averaged 0.76 cm, and egg counts were accurate within one percent. When hatching was complete, the screens were removed and dead eggs remaining on the screens were counted. Eggs were introduced to the 4 gravel boxes at the same time, in 8 horizontal layers about 5 cm apart.

Gravel used in the channels and the boxes consisted of sorted pit-run gravel, fairly sharp-edged in form. Mean particle diameter was 2.36 cm. Size distribution, obtained from twelve 3-kg samples, with a standard set of non-metric Tyler 7 in dia. (18 cm) metal sieves, was as follows.

Class (in)	<.25	.25- .50	.50- .75	.75-1.00	1.00-1.25	1.25-1.50
Approx. equiv. (mm)	<6.5	6.5-12.5	12.5-19.0	19.0-25.4	25.4-31.7	31.7-38.1
Proportion	.000	.007	.058	.657	.276	.003

A windowless observation shed was used to work in darkness on any one unit, once the eggs had hatched. It was covered and skirted with black plastic, 2.4 m long by 1.8 m wide and 1.8 m high, and ran on tracks the length

of the channels. To use, the shed would be positioned over the required unit, the observer would enter and close the door. After lifting and stacking the required number of covering planks, he could work in darkness sufficiently deep to keep fish calm and yet obtain, aided by a shielded flashlight, fish or water samples, or observe the fish directly. What little light was present within the shed did not appear to perturb the fish, indicating that it affected the fish no more than the light presumably always visible during daylight hours through cracks in and among the planks. Strips of black plastic had been stapled along one side over the gaps between the boards, but these proved non-durable and were often disturbed by wind or human activities.

A third group of eggs was divided into 24 lots of 200 each. Each lot was put, in gravel, in a 15 cm dia. by 15 cm high sampler cage, made of 8-mesh stainless steel screening. The samplers were set out in pairs in 12 different locations in the channels to measure certain effects on brood kept captive throughout the incubation phase in precisely delimited locations. Locations were immediately above, halfway down, and just below the fish-holding sections of all four channels (Fig. 1).

Fish were hand counted upon emergence and samples preserved in 5% formalin. Samples were processed some 6 wk following preservation, when fork lengths, to the nearest 0.2 mm, and total wet weights, to the nearest mg, were taken in the laboratory. Stage of development was indexed as usual, by K_D-index (Bams 1970), expressed as

$$K_D = \frac{10 \sqrt[3]{\text{weight in mg}}}{\text{length in mm}} .$$

The experimental design (Fig. 1) was a replicated, incomplete factorial design, incorporating 3 factors at 2 or 3 levels, plus an inadvertent metabolites gradient along each channel. Density of eggs and alevins ($D_{1,2,3}$) was selected at 0.5, 1.0, and 2.0 times the usual Japanese loading rates. This equated with respectively, 6,000, 12,000, and 24,000 eggs per square meter, or, 6.6, 13.2, and 26.4 thousand per unit. Flow rates ($F_{1,2}$) were set at normal and double the usual Japanese rates, so that the "standard" density and flow relationship was represented also at the higher density. The third factor was depth of gravel ($G_{1,2}$), where G_1 corresponded to a "standard", almost complete single layer of gravel, and G_2 was a 6 cm deep layer extending from screen to screen.

The fourth environmental "factor" was the compound gradient in metabolite levels associated with the linear sequence of the units in a channel. An increasing number of "egg-units" (EU, set equal to multiples of 6.6 thousand eggs present) affected the water progressively downstream. The changes were unlikely to be linearly additive due to molecular exchange with surface air, gravel, and concrete. The EU values spanned a range of 0.5 to 13.5 in the centers of the experimental units, and from 0 to 14 in the sampler locations. Replicates for each of the 10 treatment combinations were always located 7 EU's apart, but unavoidably, pairs had different means, cf. Fig. 1.

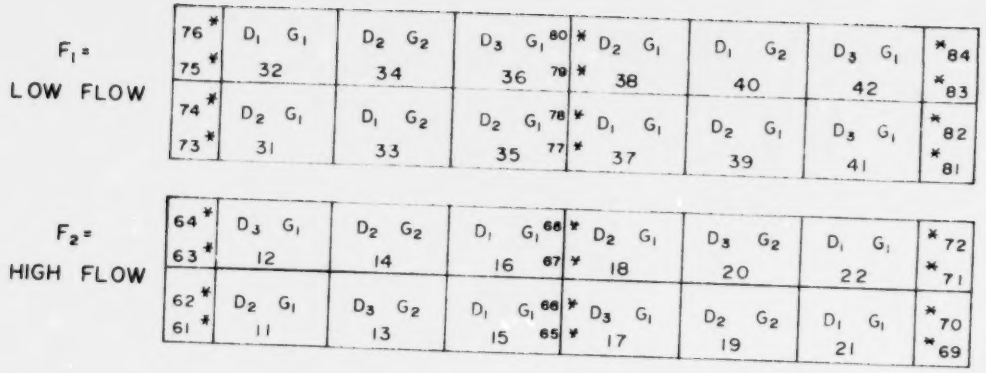

Fig. 1. Plan of the two subdivided incubation channels, showing all treatments, units, and samplers. Waterflow was to the right. $F_{1,2}$ = flow 1, 2 = 40, 80 Lpm, each half channel; $D_{1,2,3}$ = fish density 1, 2, 3 = 6, 12, 24,000 eggs per m^2; $G_{1,2}$ = gravel depth 1, 2 = single, 6-cm deep layer; * = sampler location; # = unit or sampler code number.

RESULTS

EGGS AND ALEVINS

Eggs: Average total mortality was 13.8% up to time of planting. Counts of live eggs planted in all units are given in Table 1. Where known, mortalities incurred to hatching are included and the net live counts used for further calculations. Significant pre-hatch mortalities only occurred in four high density units (where eggs were up to four layers deep), at the low flow rate; the range was from 5.3 to 22.0% with a mean of 15.5%. Evidently, water exhange was insufficient under these conditions and almost total mortality was observed in the more central areas of the egg masses. Mortalities were less than one half percent at the high density at twice the flow rate and at all lower densities at both flow rates.

Alevins: Upon hatching, alevins dropped through the hatching screens and distributed themselves, at least initially, evenly over the available area. Fish could be seen among the stones at all densities in the shallow gravel. In the 6-cm deep gravel they almost entirely disappeared from view at the lower two densities, but about half were visible at the high density. Evidently, fish bodies filled the crevices among the stones entirely. Spontaneous movement was observed, in which a group of closely congregated fish would move in unison, mostly in a head-down position ("digging"), rearrange the grouping among themselves, and settle down again. The preferred rest position was back up, head somewhat down from horizontal, bodies aligned in parallel, and arranged in groups as determined by geometry of the gravel. In older alevins (yolk sac half absorbed) more horizontal movement was observed and "clumping", i.e. unstable grouping at greatly increased densities, would occur. At the high flow rate the direction was primarily upstream; at the low flow fish moved in both directions. Very heavy concentrations of fish would dissipate in time, but as a rule, once formed, higher density areas tended to remain until close to swim-up. Such behavioral phenomena undoubtedly contributed to the substantial variance observed in many characteristics associated with fish rearing in these units. Clumping was not observed at the two lower densities at the low flow rate.

Approaching time of swim-up, activity increased in all units. Activity increased particularly at the higher densities where, especially following a disturbance such as momentary illumination with a flashlight, fish would congregate in corners and along both screens. All available spaces in the gravel would then be filled with fish and others would be trying to dig down in among them. In such areas the gravel could be hidden from view entirely with a solid layer of fish. Gradually, more and more fish would remain above the gravel. Initially most would be heavier than water and remain near the bottom, but gradually more would become neutrally buoyant and very slowly swim about the unit in the supragravel water. After a long period of quiet, many fish would have congregated near the bottom screens. Evidently such fish had been holding position in the current while slowly drifting downstream. When disturbed, a net upstream movement would result in redistribution.

Table 1. Numbers of eggs and alevins contained in all experimental units, and egg mortality where known. Also shown are remaining treatment conditions.

Unit no.	No. eggs planted	Dead eggs No.	Dead eggs %	No. alevins	Flow lpm	Gravel[a] depth	EU[b]
11	12,960	18	.14	12,942	80	1	1.0
12	25,920	64	.25	25,856	80	1	2.0
13	25,920	102	.39	25,818	80	2	4.0
14	12,960	44	.34	12,916	80	2	5.0
15	6,480	10	.15	6,470	80	1	6.5
16	6,480	14	.22	6,466	80	1	6.5
17	25,920	49	.19	25,871	80	1	9.0
18	12,960	18	.14	12,942	80	1	8.0
19	12,960	27	.21	12,933	80	2	12.0
20	25,920	75	.29	25,845	80	2	11.0
21	6,480	16	.25	6,464	80	1	13.5
22	6,480	12	.19	6,468	80	1	13.5
31	12,960	34	.26	12,926	40	1	1.0
32	6,480	24	.37	6,456	40	1	0.5
33	6,480	9	.14	6,471	40	2	2.5
34	12,960	64	.49	12,896	40	2	2.0
35	25,920	5700	22.0	20,220	40	1	5.0
36	25,920	3765	14.5	22,155	40	1	5.0
37	6,480	10	.15	6,470	40	1	7.5
38	12,960	40	.31	12,920	40	1	8.0
39	12,960	37	.29	12,923	40	2	9.0
40	6,420	11	.17	6,469	40	2	9.5
41	25,920	1369	5.3	24,551	40	1	12.0
42	25,920	5192	20.0	20,728	40	1	12.0
Box 1	16,000	-	-	-	8	d	1.3
Box 2	32,000	-	-	-	16	d	2.7
Box 3	32,000	-	-	-	16	d	2.7
Box 4	16,000	-	-	-	8	d	1.3
Samplers	200	(1.2)	(.6)	(198.8)	-[c]	d	-[c]

[a] 1 = single layer; 2 = 6 cm deep layer; d = deep substrate.
[b] EU = "egg units" = number of eggs upstream of centre of unit.
[c] 24 samplers were located in different parts of both channels, see text.

Fish tended to resist being sucked into the exit tubes. Coming near them they would perceive the backward acceleration and try to swim away. Sheer pressure from adjacent fish would force many of them down anyway, but it was obvious that unlike fish emerging from gravel boxes, many remained in these units without "emerging" for many days following achieving neutral buoyancy. Feeding and schooling behaviour developed among such fish and eventually they had to be forcefully removed from the units for enumeration. It may safely be assumed that emergence would have been earlier from channels with unimpeded (unscreened) exits.

SURVIVAL TO EMERGENCE

Survival from time of hatching to emergence was high in all units (Table 2), almost all were 95% or better. There were some difficulties with these data. Two data points were adjusted following accidental losses; units 19 and 39 were assigned the group mean value for their level of density and flow. Also, some fish moved between units. This was clear from hundreds of fish occurring in the unused channel sections above the units, some survivals exceeding 100%, and from direct observation. At the early alevin stage, fish in the high flow section were seen on occasion to penetrate the 8-mesh dividing screens when a disturbance had concentrated the fish against a screen. Once a fish's head protruded through the screen, the pressure exerted by adjacent fish would gradually force its body and yolk sac through, until it could extricate itself by vigorous swimming. If universal among all units, the effect would be expected to increase in frequency with increasing density and, relatively, with density differential. This expectation was born out by a Kendal correlation test ranking the units at each flow in order of increasing numbers of fish present in the two units adjacent to them. At the low flow there was virtually no correlation, $\tau=-.12$, $P>.2$, but at the high flow the effect was pronounced and statistically significant, $\tau=.56$, $P<.01$. The data are insufficiently precise, however, to calculate a correction factor that could improve the sensitivity of the survival data, and hence, the data are evaluated at face value.

As the following text table shows, group survival means showed a marginal increase with increased flow, and a decrease with increased density.

F_1:	D_1	97.33%	F_2:	D_1	100.80%
	D_2	98.20%		D_2	100.26%
	D_3	97.15%		D_3	97.50%

However, no differences associated with flow (2 levels), density (3 levels), and depth of gravel (2 levels) were significant ($P>.2$) when tested by Student-t test on all available paired observations.

Survivals in the upwelling boxes were all very high, between 98.0 and 99.9 percent, with means of 99.7 and 98.7 for the low and high density units.

Table 2. Survival (%), from egg to fry, in all channel (no. 11-42) and box (no. 1-4) units.

	Flow 1				Flow 2			
	G_1		G_2		G_1		G_2	
Density 1	(32)[f]	97.5	(33)	97.2[a]	(15)	114.4[b]		-
					(16)	96.1		-
	(37)	97.4	(40)	97.2[a]	(21)	95.0		-
		-	(1)	99.5	(22)	97.7		-
Box		-	(4)	99.9		-		-
Density 2	(31)	97.3	(34)	97.6[a]	(11)	101.7[c]	(14)	97.9
	(38)	99.7	(39)	88.1 [98.2][ad]	(18)	101.2[c]	(19)	88.1[e]
		-		-		-	(2)	98.0
Box		-		-		-	(3)	99.5
Density 3	(35)	93.5		-	(12)	93.2	(13)	99.8
	(36)	98.5		-				
	(41)	95.9		-	(17)	95.4	(20)	101.6
	(42)	100.7		-				

[a] Unit situated upstream from treatment $D_3G_1F_1$.
[b] Unit situated upstream from treatment $D_3G_1F_2$.
[c] Unit situated upstream from treatment $D_3G_2F_2$.
[d] Incomplete count, dummy ($\bar{x}$ D_2F_1) value in brackets.
[e] Confounded test, value considered to be a minimum.
[f] Unit numbers are in brackets.

Codes on all tables are as follows:

$D_{1,2,3}$ = Density 1,2,3 = 6, 12, 24 thousand eggs per square meter.
$F_{1,2}$ = Flow 1,2 = 40, 80 lpm for each channel half.
$G_{1,2}$ = Gravel depth 1,2 = single, 6 cm deep layer.

Survival to the fry stage in the 24 sampler baskets, located in duplicate in 12 different locations in the channels and holding 200 eggs each, ranged from 99.0 to 100.0%, $\bar{X}$ =99.65, in the high flow channel, and from 96.0 to 102.0%, $\bar{X}$ =99.33, in the low flow one. There were only two data points below 99% and these occurred in the low flow channel at a middle and a bottom end location.

FRY EMERGENCE

Emergence patterns differed considerably among channel units and gravel boxes in response to all factors in the experiment. Fry migration rates from the channel units on a daily basis were affected by changing flow rates through the exit tubes and, towards the end, by the fish being scooped from their units, cf. Methods section. Rate comparisons are made therefore on selected segments of the "runs". The proportions of fish migrating from each unit during two successive segments, up to April 4 and from April 5-17, are given on Table 3. These and subsequent data are recorded in matrix form, all arranged by flow (2 levels), gravel depth (2 levels), and density (3 levels). Each proportion (or other datum) is preceded, in brackets, by the unit number.

Consistent differences were evident among various treatments, but most were not significant by ANOVA, Fig. 2, Table 4. Comparison 1 (Table 4) shows a decreasing proportion of fish emerged at the low flow rate (F_1) with increasing density. However, a seemingly erratic pattern existed at the high flow (F_2). Not surprisingly, the interaction term is significant at P=.1. Flow rate and, especially, gravel depth affected emergence signficantly in comparisons 2 to 4. Emergence tended to be decelerated (but not significantly so) by increased density, but was strongly decelerated by increased gravel depth. Results were similar for emergence patterns of the second release period; i.e. there was no significant effect of density; an appreciable but insignificant (P>.25) increase with increased flow; and a substantial decrease in all cases with the deep gravel, significant at P<.025 at F_2 (F=15.924 df. 1,4), but insignificant at F_1 (F=.341, df. 1,4). Late emergence was also associated with the deep gravel at the high flow, G_2F_2. This is also clearly demonstrated on Table 5, where the "median day" of fry emergence, $\bar{X}$, is April 11 for $D_{2,3}$ in G_1; but $\bar{X}$ for $D_{2,3}$ in G_2 is April 16. Similarly, mean percentages of fry emerged on April 14 were, respectively, 72 and 45%.

Significant differences are observed between replicates of all density and flow combinations when paired by location in the channel. The experimental design put all pairs of replicates 3 experimental units apart in the direction of flow, each time containing 7.0 EU's as defined on p. 4. These upstream/downstream pairs show the following significant differences in proportions emerged during the second period.

1. At G_1 only: n=8 pairs; $\bar{X}$ (upstream)=.599, $\bar{X}$ (downstream)=.500; t=2.627, .05>P>.02 (two-tailed).

2. At $G_{1,2}$ combined: n=12 pairs; $\bar{X}$ (upstream)=.554, $\bar{X}$ (downstream)=.454; t=2.793, .02>P>.01 (two-tailed).

Table 3. Proportions of total fry emerged from all channel units, during two periods, up to April 4 and from April 5 to 17, 1980.

	Flow 1						Flow 2					
	G_1			G_2			G_1			G_2		
Density 1	(32)	.177	.580	(33)	.107	.624	(15)	.212	.726		-	
							(16)	.122	.756		-	
	(37)	.206	.518	(40)	.110	.292	(21)	.089	.589		-	
							(22)	.058	.444		-	
Density 2	(31)	.182	.547	(34)	.112	.440	(11)	.273	.592	(14)	.125	.358
	(38)	.108	.389	(39)	.134	.460	(18)	.219	.515	(19)	.140	.398
Density 3	(35)	.124	.544		-		(12)	.132	.508	(13)	.119	.434
	(36)	.124	.537		-							
	(41)	.114	.476		-		(17)	.222	.515	(20)	.062	.299
	(42)	.139	.557		-							

Unit numbers are in brackets.

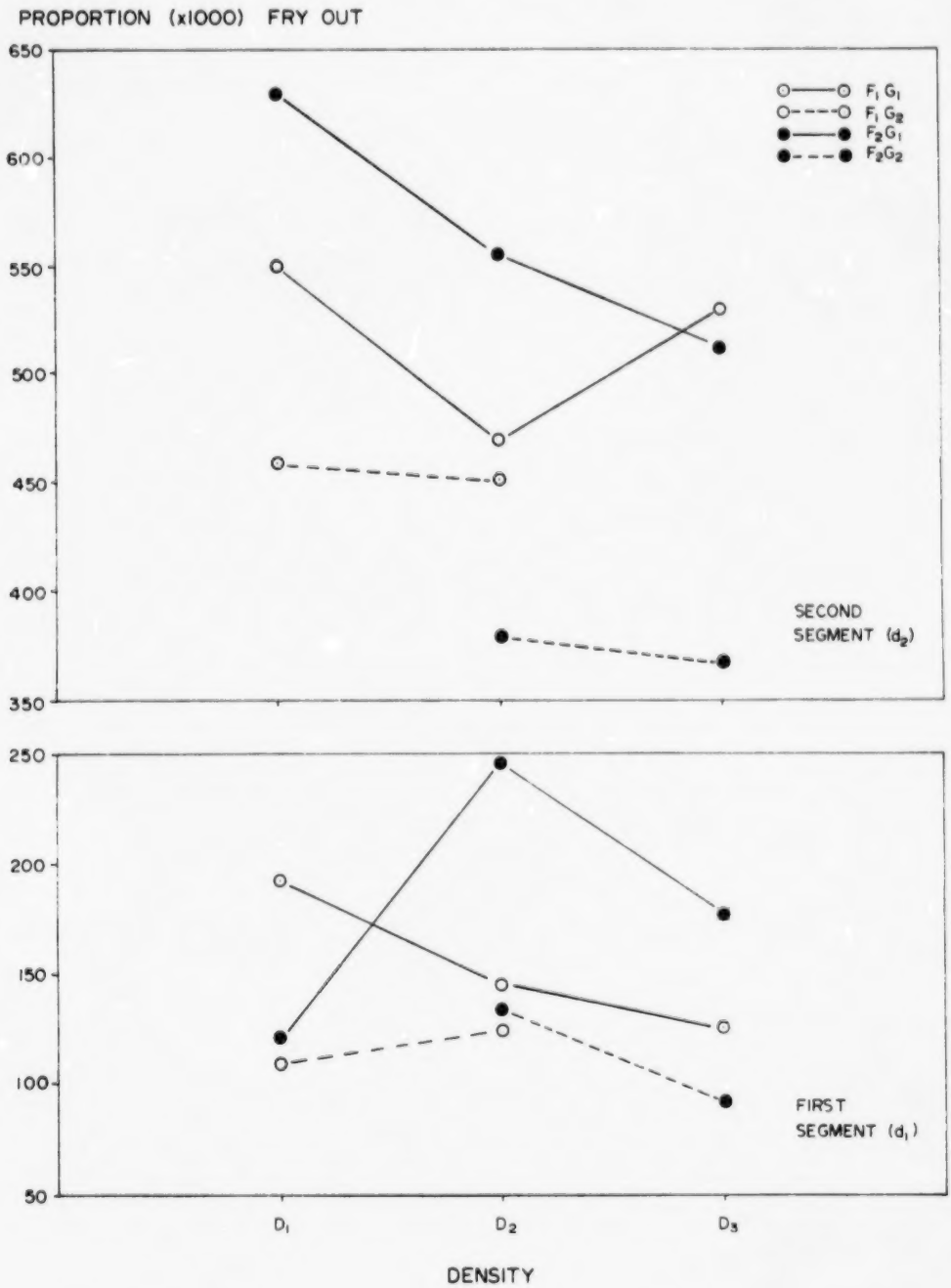

Fig. 2. Proportions of fry emerged from all 10 treatment combinations during two time segments, arranged by fry density.

Table 4. Fry emergence, as mean proportions of total migrations, during the first part of the migration period, and ANOVA's (data x 1000), on different treatment combinations in the channels.

1.	TMT = $D_{1,2,3,\bar{X}}$	.192	.145	.126	.154	at G_1
	BLK = $F_{1,2,\bar{X}}$	.121	.246	.177	.181	
	REP = 2	.156	.196	.152	.168	
		SS	df	MS	F	
	TMT	4,689	2	2,344	1.082	.50>P>.25 NS[a]
	BLK	2,187	1	2,187	1.009	.50>P>.25 NS
	INT	15,656	2	7,828	3.613	.10>P>.05 +
	ERR	12,999	6	2,167		
	TOT	35,531	11			
2.	TMT = $F_{1,2,\bar{X}}$	.145	.246	.196		at D_2
	BLK = $G_{1,2,\bar{X}}$	.123	.133	.128		
	REP = 2	.134	.189	.162		
	TMT	6,105	1	6,105	5.367	.10>P>.05 +
	BLK	9,180	1	9,180	8.070	.05>P>.025 *
	INT	4,186	1	4,186	3.680	.25>P>.10 NS
	ERR	4,551	4	1,138		
	TOT	24,022	7			
3.	TMT = $D_{1,2,\bar{X}}$	.192	.145	.168		at F_1
	BLK = $G_{1,2,\bar{X}}$	.109	.123	.116		
	REP = 2	.150	.134	.142		
	TMT	512	1	512	0.601	.50>P>.25 NS
	BLK	5,513	1	5,513	6.476	.10>P>.05 +
	INT	1,861	1	1,861	2.186	.25>P>.10 NS
	ERR	3,405	4	851		
	TOT	11,290	7			
4.	TMT = $D_{2,3,\bar{X}}$	.246	.177	.212		at F_2
	BLK = $G_{1,2,\bar{X}}$	.133	.091	.112		
	REP = 2	.189	.134	.162		
	TMT	6,161	1	6,161	3.401	.25>P>.10 NS
	BLK	20,000	1	20,000	11.042	.05>P>.025 *
	INT	365	1	365	0.201	.75>P>.50 NS
	ERR	7,245	4	1,811		
	TOT	33,770	7			

[a]On all ANOVA tables: + = .10 > P > .05; * = .05 > P > .01; ** = .01 > P.
TMT = treatment; BLK = block; INT = interaction; ERR = error; TOT = total; REP = replications. Treatments form columns; Blocks form rows.

Table 5. Day (date in April) of median fry emergence (first column after unit number) and percentage of run emerged on April 14, 1980, (second column) of all channel and box units.

	Flow 1						Flow 2					
	G_1			G_2			G_1			G_2		
Density 1	(32)	11	74	(33)	11	70	(15)	10	94		-	
							(16)	11	88		-	
	(37)	11	72	(40)	21	39	(21)	11	67		-	
							(22)	17	49		-	
Box		-		(1)	18	8.9		-			-	
		-		(4)	21	0.3		-			-	
Density 2	(31)	11	71	(34)	12	54	(11)	10	85	(14)	18	46
	(38)	18	47	(39)	10	69	(18)	11	73	(19)	14	51
		-			-			-		(2)	20	0.9
Box		-			-			-		(3)	20	1.0
Density 3	(35)	11	64		-		(12)	12	57	(13)	14	52
	(36)	12	62		-							
	(41)	12	58		-		(17)	11	72	(20)	19	32
	(42)	12	65		-							

Unit numbers are in brackets.

Similar but smaller differences also existed in the fish migrating during the first time period, but these were not significant (t=.994 and 1.032; df.=7 and 11; .4>P>.2, two-tailed). The differences between these paired proportions showed a considerable range. Rank analysis confirmed a decrease in magnitude with increasing density, but consistent effects were not present as a function of either flow, gravel depth, or EU's.

Emergence from the gravel boxes was significantly later than from the channel units, even though accumulated temperature units were the same (Table 5). For example, of the 24 channel units 18 showed 50 to 88% emergence by April 14, with the remainder having reached 38 to 49%. At this time the boxes had reached only 0.3 to 8.9%, mean 2.8%, and none reached their median levels before April 18 to 21, i.e. from 4 to 7 days later than the channel units. An unexpectedly large difference in mean time of emergence occurred between the two low density boxes. Their mean (coded) emergence dates were 48.9 and 52.1 (.95 limits $\pm$.04), while the two high density boxes were identical at 51.3 (.95 limits $\pm$.03).

An attempt is made to pull these often diverse, and possibly bewildering, responses in fry emergence timing together in the Discussion, below.

ALEVIN AND FRY LENGTHS

Differences in mean lengths among fish from all 10 channel treatment combinations, based on 24 samples per sampling date, were present from the first sampling day, but were never large, Tables 6, 7. For example, on day 01 (=March 13, 24 days following mean hatching) the ten means had a range, in mm, of 29.55 $\pm$ .18 or 1.22% of the midpoint; 2 wk later, on day 15, it had doubled to 33.33 $\pm$ .40, or still only 2.40%. During the early part of the fry run, measured on days 22, 24, and 27, it decreased again among the fish that migrated to 35.11 $\pm$ .24 or 1.38%, and during the middle of the run, days 30, 31, and 35, it reduced even further, to only 36.35 $\pm$ .14 or .78%. Among sampling dates, mean lengths increased rapidly due to growth. This is indicated by the range midpoints given above, which show daily mean growth increments of 0.270, 0.198, and 0.155 mm for the three intervening periods, also see Fig. 10. The larger size differences associated with the treatments, therefore, were equivalent to about 5 to 10 days' growth.

The effects of density, flow, and gravel depth on fish length are complex and often interactive. A useful overview emerges from plots of averaged sample means lumped by successive sample days, Figs. 3 and 4. At the alevin stage fish from the fast flow (F_2) units show superior length over the low flow (F_1) ones, with the exception of the high density, shallow gravel (D_3 G_1) units, where fish were notably less developed. The tendency remained among the fry migrants, but the shallow gravel, slow flow (G_1 F_1) fish caught up at all but the middle densities.

The deep gravel units at the high flow rate (G_2 F_2) produced consistently superior sizes, whereas the low flow, deep gravel (F_1 G_2) units were equally consistently inferior compared to all the rest. Clearly, the

Table 6. Mean lengths, in mm, of alevins from all channel units on days 01 (March 13, 1980) and 15. Also given are (mean) treatment ranks, by date.

	Flow 1				Flow 2			
	G_1		G_2		G_1		G_2	
Density 1	(32) 29.04	33.35	(33) 29.40	33.62	(15) 29.63	33.05	-	
					(16) 29.59	33.60	-	
	(37) 29.74	33.26	(40) 29.38	33.01	(21) 29.89	33.31	-	
					(22) 29.81	33.59	-	
Rank	2 1/2	4 1/2	2 1/2	4 1/2	10	6		
Density 2	(31) 29.73	33.26	(34) 29.26	32.98	(11) 29.45	33.50	(14) 30.07	33.38
	(38) 29.58	33.16	(39) 29.78	33.54	(18) 29.89	33.95	(19) 29.32	33.46
	7	2	4 1/2	3	7	10	9	8
Density 3	(35) 29.15	33.43	-		(12) 29.40	32.87	(13) 29.57	33.53
	(36) 29.36	33.45	-					
	(41) 29.60	33.36	-		(17) 29.34	32.99	(20) 29.78	33.76
	(42) 29.83	33.39	-					
	4 1/2	7			1	1	7	9

Unit numbers are in brackets.
Ranges: 29.37 to 29.73 = 29.55 $\pm$ .188 mm and 32.93 to 33.73 = 33.33 $\pm$ .40 mm.

Table 7. Mean alevin lengths, in mm, and ANOVA's on various treatments on sampling day 15. All squares x 1000.

1. TMT = $D_{1,2,3,\bar{X}}$
BLK = $F_{1,2,\bar{X}}$
REP = 2

33.305	33.210	33.410	33.308	at G_1
33.390	33.725	32.930	33.348	
33.348	33.468	33.170	33.328	

	SS	df	MS	F		
TMT	1792	2	896	4.250	.10>P>.05	+
BLK	48	1	48	0.028	.75>P>.50	NS
INT	4981	2	2490	11.811	.01>P>.005	**
ERR	1205	6	211			
TOT	8086	11				

2. TMT = $G_{1,2,\bar{X}}$
BLK = $F_{1,2,\bar{X}}$
REP = 2

33.210	33.260	33.235	at D_2
33.725	33.420	33.573	
33.468	33.340	33.404	

TMT	325	1	325	0.488	.75>P>.50	NS
BLK	2278	1	2278	3.423	.25>P>.10	NS
INT	630	1	630	0.947	.50>P>.25	NS
ERR	2663	4	666			
TOT	5896	7				

3. TMT = Up/Down, $\bar{X}$
BLK = $D_{1,2,3,\bar{X}}$
REP = 2

33.440	33.705	33.573	at F_2
33.200	33.375	33.288	
33.325	33.450	33.388	
33.322	33.510	33.416	

TMT	1064	1	1064	0.767	.50>P>.25	NS
BLK	1673	2	1836	0.603	.75>P>.50	NS
INT	101	2	50	0.036	P>.75	NS
ERR	8320	6	1387			
TOT	11157	11				

Table 7. (cont'd)

4. TMT = $D_{1,2,\bar{X}}$ 33.305 33.210 33.258 at F_1
BLK = $G_{1,2,\bar{X}}$ 33.315 33.260 33.288
REP = 2 33.310 33.235 33.273

	SS	df	MS	F		
TMT	113	1	113	0.128	.75>P>.50	NS
BLK	18	1	18	0.020	P>.75	NS
INT	8	1	8	0.009	P>.75	NS
ERR	3519	4	880			
TOT	3658	7				

5. TMT = $D_{2,3,\bar{X}}$ 33.725 32.930 33.328 F_2
BLK = $G_{1,2,\bar{X}}$ 33.420 33.645 33.533
REP = 2 33.573 33.288 33.430

TMT	1625	1	1625	4.705	.10>P>.05	+
BLK	841	1	841	2.434	.25>P>.10	NS
INT	5202	1	5202	15.067	.025>P>.01	*
ERR	1381	4	345			
TOT	9048	7				

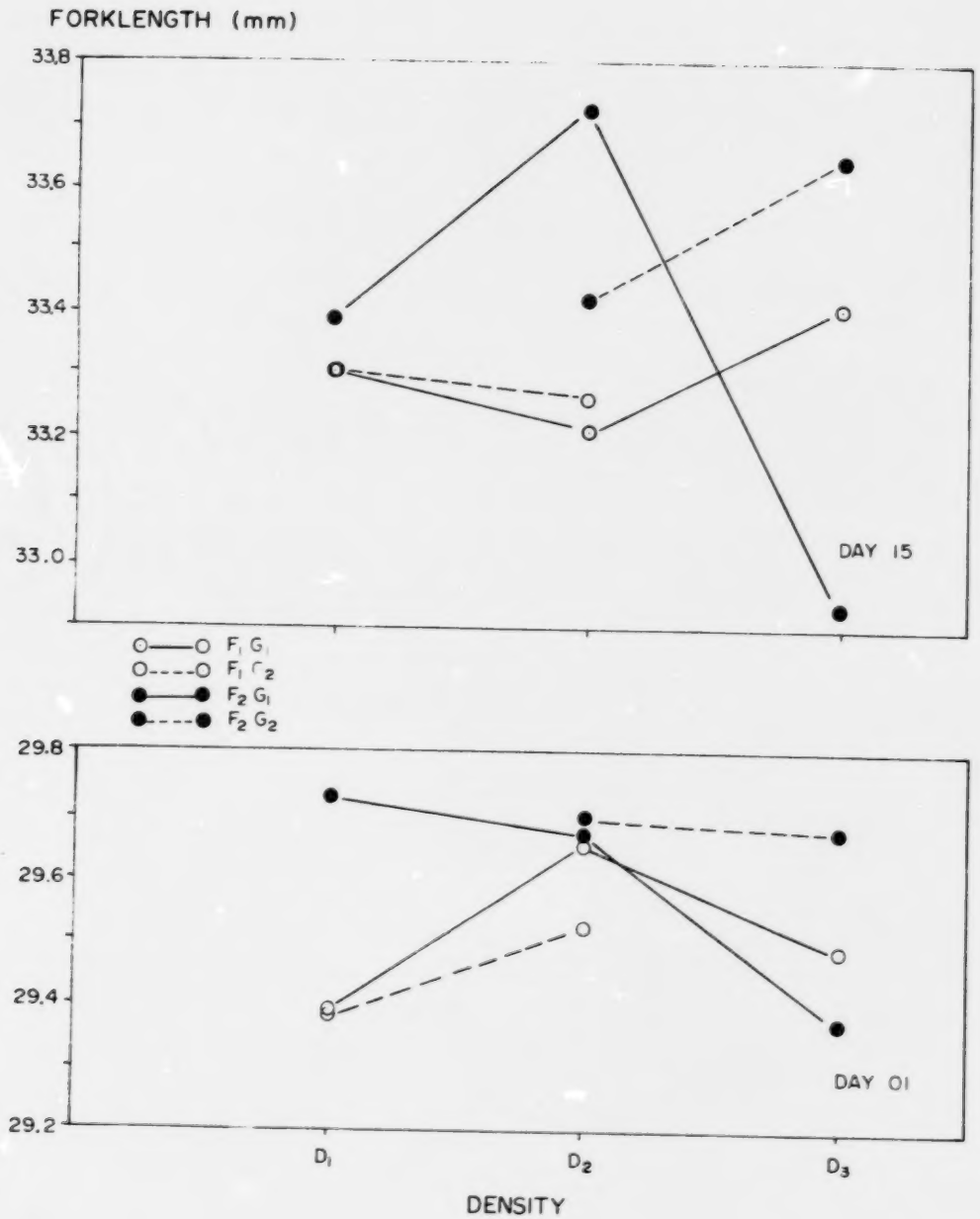

Fig. 3. Alevin mean lengths, on two dates, for all 10 treatment combinations, by density. Day 01 was the 25th day following mean hatching.

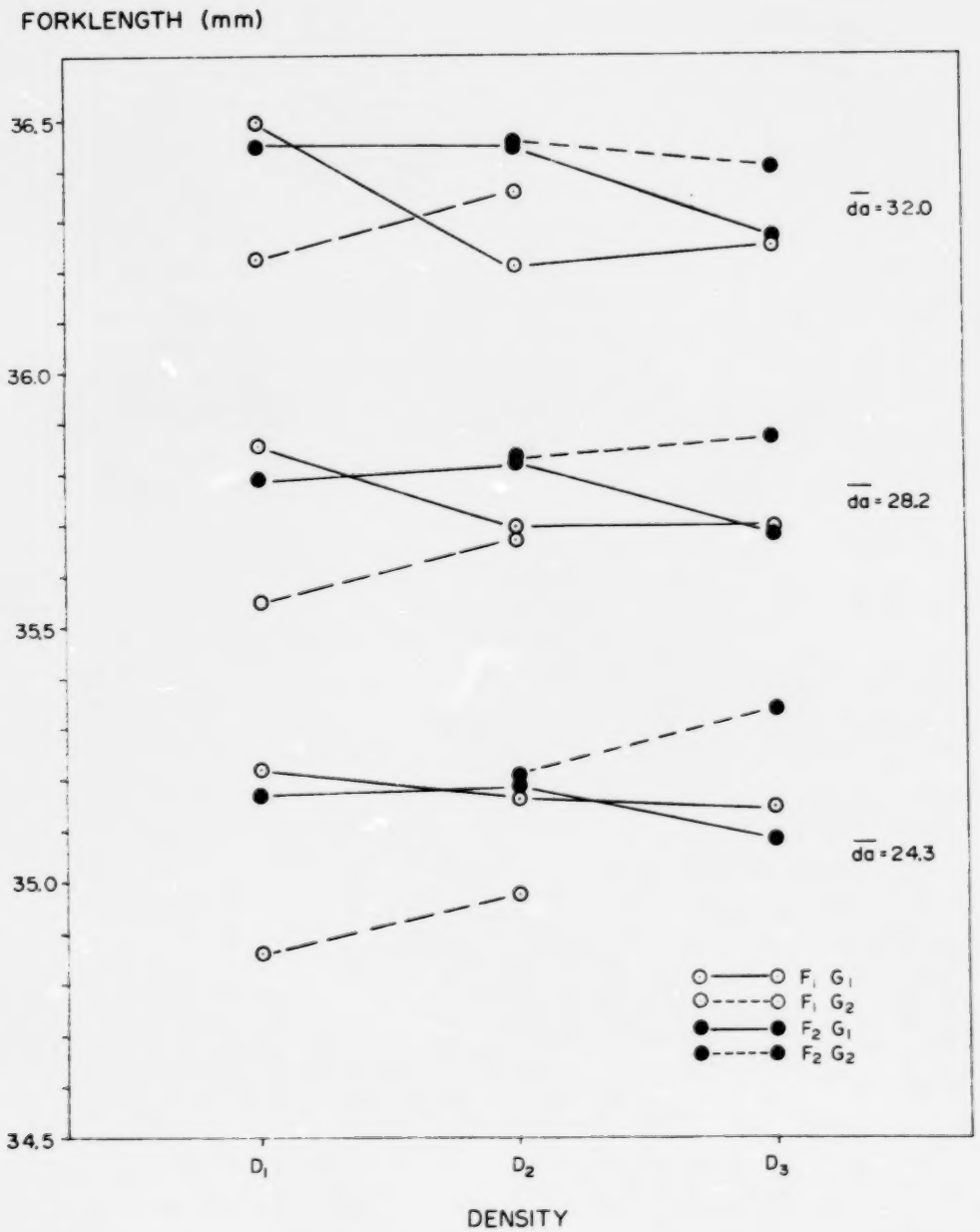

Fig. 4. Fry mean lengths, on three averaged dates, for all 10 treatment combinations, by density.

deeper substrate level can be advantageous in terms of growth, but only at a much higher than normal flow rate.

Positive correlation exists between fish density and body size in the deep gravel (G_2) at both flow rates. The shallow gravel (G_1) on the other hand showed no correlation or a weak tendency toward the expected negative correlation with density.

Analyses of variance showed most of the observed differences to be statistically insignificant, Tables 7, 10, and these differences must be considered as trends only.

There was no evidence of any upstream/downstream effect on size, in 12 pairs of replicates 7 EU's apart, both in the alevins at day 15, and in the fry at the two groups of days as recorded on Table 9. The differences between the means of each of the paired groups were 0.063 mm or less, and student-t values ranged from -.725 to +.618, df=11, all P's>0.4.

Mean lengths of fish from the sampler baskets showed a statistically significant ($P<.01$) response to location in the channel (Fig. 5; Table 8). Mean lengths decreased with increasing cumulative density in both flows, but strongly so only in the low flow (F_1) treatment. The effect of an increase in flow rate is clearly interactive, length decreasing at low density but increasing at high density. As would be expected, the downstream gradient has a much greater effect on growth at the low flow rate (F_1) than at the high rate (F_2).

All mean lengths obtained in the samplers exceeded those in the channel units, cf. Fig. 5 with Fig. 4, middle set of data. Although differences among locations were significant, the range of sizes was still small. For the means of the six locations it comprised only 0.5 mm, or about 1.5% of the overall mean.

Gravel-box fry, on average, emerged later than channel fry and were larger, Table 11, Figs. 6 and 7. Over almost the entire period of emergence, box fry mean lengths ranged from an average 36.06 mm on day 33 to 37.30 mm on day 43, while channel fish ranged from 34.89 on day 22 to 36.78 on day 43. Among the box fry the high density, high flow (D_2 F_2) fry were somewhat larger than the low density, low flow (D_1 F_1) ones, but the difference was statistically not significant.

Fish from the gravel boxes can be compared with those from channel units corresponding closest in density and flow characteristics, i.e treatments D_2F_1 and D_3F_2. Averaged over the entire emergence period, box fry were consistently larger than the channel fry. On average, at the two densities and on the unweighted means, the box fry were larger by respectively 2.5 and 2.8% (Fig. 6); on the weighted, for abundance, means by 1.8 and 1.5% (Fig. 7).

Alevin and Fry Weights

Fish weights were more variable than fish lengths and differences between groups were generally even less significant statistically than those

Table 8. Mean lengths (mm), weights (mg), and developmental indices (K_D) of fry from sampler baskets, and 2-way ANOVA's.

1. TMT = $EU_{0,7,14,\bar{X}}$
BLK = $F_{1,2,\bar{X}}$
REP = 4

36.42	36.24	35.90	36.19	Length in mm
36.25	36.18	36.13	36.18	
36.33	36.21	36.02	36.19	

	SS	df	MS	F	P	
TMT	405	2	203	6.223	.01>P>.005	**
BLK	0	1	0	0.001	P>.75	NS
INT	169	2	85	2.595	.25>P>.10	NS
ERR	586	18	33			
TOT	1,161	23	All squares x 1000			

2. TMT = $EU_{0,7,14,\bar{X}}$
BLK = $F_{1,2,\bar{X}}$
REP = 4

416.3	412.7	409.5	412.8	Weight in mg
411.0	409.4	407.9	409.4	
413.7	411.0	408.7	411.1	

TMT	986	2	493	1.350	.50>P>.25	NS
BLK	704	1	704	1.927	.25>P>.10	NS
INT	135	2	68	0.185	P>.75	NS
ERR	6,575	18	365			
TOT	8,401	23	All squares x 10			

3. TMT = $EU_{0,7,14,\bar{X}}$
BLK = $F_{1,2,\bar{X}}$
REP = 4

2.039	2.042	2.057	2.046	K_D-value
2.040	2.040	2.040	2.040	
2.040	2.041	2.048	2.043	

TMT	354	2	177	2.401	.25>P>.10	NS
BLK	198	2	170	2.307	.25>P>.10	NS
INT	340	2	170	2.307	.25>P>.10	NS
ERR	1,325	18	74			
TOT	2,217	23	(data-2) x 1000			

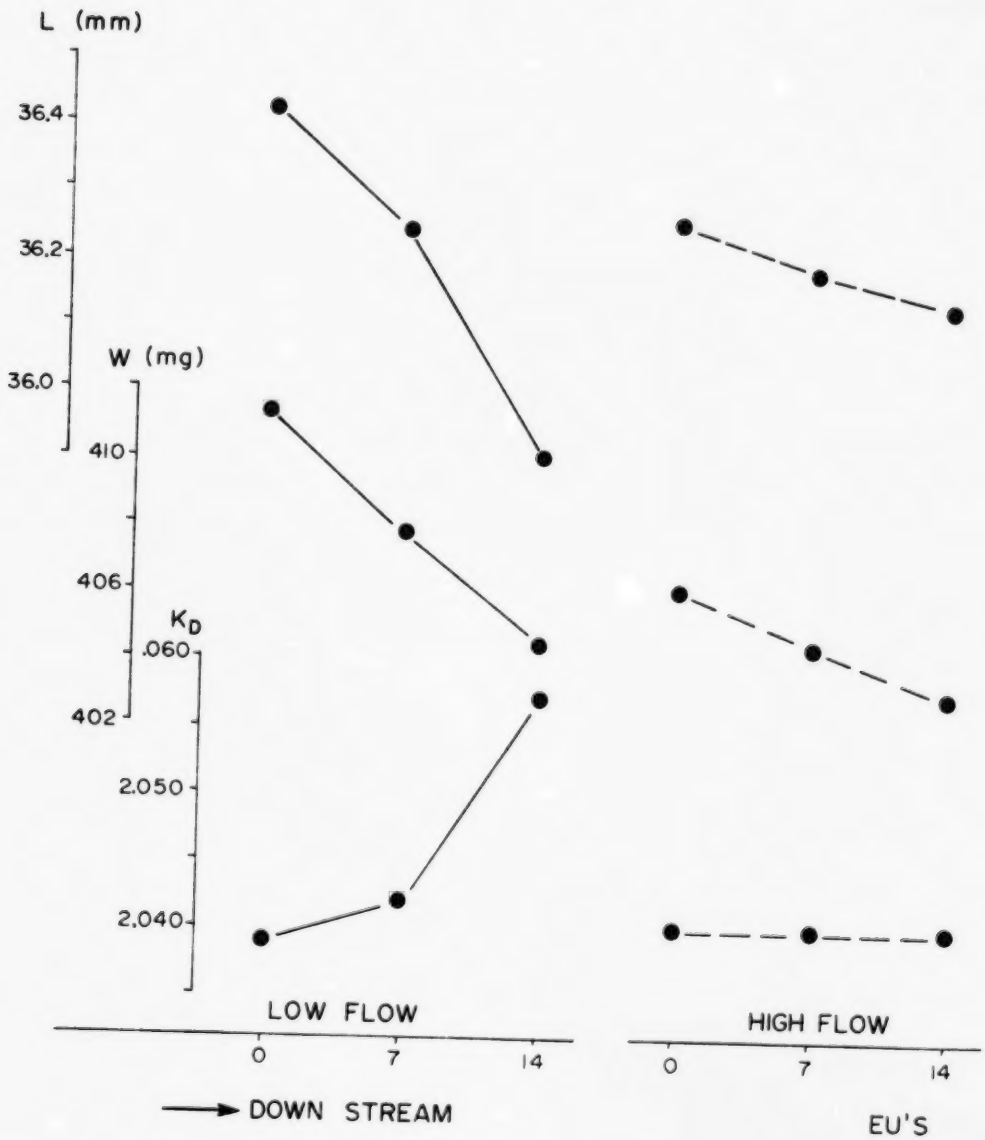

Fig. 5. Mean fork lengths (L), total wet weights (W), and developmental indices (K_D) of fish from all sampler baskets, on day 28, by flow and EU-values (where 1 EU = 6,600 eggs incubating upstream of sampler location).

Table 9. Mean lengths, in mm, of fry migrants from all channel units, averaged for days (22, 24, 27 and 30, 31, 35). Also given are (mean) treatment ranks, by grouped dates.

	Flow 1				Flow 2			
	G_1		G_2		G_1		G_2	
Density 1	(32) 35.30	36.41	(33) 34.91	36.23	(15) 34.90	36.30	-	
					(16) 35.11	36.45	-	
	(37) 35.14	36.58	(40) 34.82	36.22	(21) 35.41	36.53	-	
					(22) 35.24	36.37	-	
Rank	9	10	1	2	5 1/2	7		
Density 2	(31) 35.27	36.29	(34) 34.92	36.00	(11) 35.11	36.54	(14) 35.20	36.34
	(38) 34.97	36.13	(39) 35.03	36.73	(18) 35.27	36.35	(19) 35.22	36.57
	5 1/2	1	2	5	7	8	8	9
Density 3	(35) 35.14	36.21	-		(12) 35.31	36.46	(13) 35.35	36.38
	(36) 35.32	36.38	-					
	(41) 34.99	35.95	-		(17) 34.86	36.08	(20) 35.32	36.43
	(42) 35.11	36.42	-					
	4	3			3	4	10	6

Unit numbers are in brackets.
Ranges: 34.87 to 35.35 = 35.11 $\pm$ .243 mm, and 36.21 to 36.50 = 36.35 $\pm$ 143 mm.

Table 10. Mean fry lengths in mm, and ANOVA's of various treatments on combined sampling days 30+31. All squares x 1000.

1. TMT = $D_{1,2,3,\bar{X}}$ BLK = $F_{1,2,\bar{X}}$ REP = 4

	36.423	36.123	36.190	36.245	at G_1
	36.365	36.525	36.178	36.356	
	36.394	36.324	36.184	36.301	

	SS	df	MS	F		
TMT	2,944	2	1,472	2.945	.10>P>.05	+
BLK	294	1	294	0.588	.50>P>.25	NS
INT	3,597	2	1,799	3.599	.05 P	*
ERR	8,997	18	500			
TOT	15,831	23				

2. TMT = $F_{1,2,\bar{X}}$ BLK = $G_{1,2,\bar{X}}$ REP = 4

	36.123	36.525	36.324		at D_2
	36.265	36.395	36.330		
	36.194	36.460	36.327		

TMT	2,836	1	2,836	4.636	.10>P>.05	+
BLK	2	1	2	0.003	P>.75	NS
INT	743	1	743	1.214	.50>P>.25	NS
ERR	7,340	12	612			
TOT	10,919	15				

3. TMT = Up/Down, $\bar{X}$ BLK = $D_{1,2,3,\bar{X}}$ REP = 4

	36.23	36.39	36.31		at G_1+G_2, F_1
	36.10	36.29	36.19		
	36.22	36.16	36.19		
	36.18	36.28	36.23		

TMT	580	1	580	0.6616	.50>P>.25	NS
BLK	778	2	389	0.4433	.75>P>.50	NS
INT	7,611	2	381	0.4339	.75>P>.50	NS
ERR	15,785	18	877			
TOT	17,904	23	-			

4. TMT = $D_{1,2,\bar{X}}$ BLK = $G_{1,2,\bar{X}}$ REP = 4

	36.545	36.123	36.334		at F_1
	36.078	36.265	36.172		
	36.312	36.194	36.253		

TMT	552	1	552	1.031	.50>P>.25	NS
BLK	1,056	1	1,056	1.972	.25>P>.10	NS
INT	3,721	1	3,721	6.947	.025>P>.01	*
ERR	6,428	12	536			
TOT	11,758	15				

Table 10. (cont'd)

5. TMT = $D_{2,3,\bar{X}}$
BLK = $G_{1,2,\bar{X}}$
REP = 4

	36.525	36.178	36.352	at F_2
	36.395	36.320	36.358	
	36.460	36.249	36.355	

	SS	df	MS	F		
TMT	1,785	1	1,785	3.396	.10>P>.05	+
BLK	2	1	2	0.003	P>.75	NS
INT	743	1	743	1.413	.50>P>.25	NS
ERR	6,307	12	526			
TOT	8,836	15				

Table 11. Mean lengths (mm), weights (mg), and developmental indices (K_D) of gravel-box fry, at 2 densities, on 7 (6) alternate days, and ANOVA's.

1. TMT Da 33/45, $\bar{X}$	35.91	35.98	36.33	36.69	37.11	37.26	36.93	36.60	Length (mm)
BLK $D_1F_1, D_2F_2, \bar{X}$	36.20	36.41	36.23	36.81	36.81	37.35	37.61	36.77	
REP 2	36.06	36.19	36.28	36.75	36.96	37.30	37.27	36.69	

	SS	df	MS	F	P	
TMT	6,397	6	1,066	12.455	.001>P	***
BLK	209	1	209	2.443	.25>P>.10	NS
INT	637	6	106	1.241	.50>P>.25	NS
ERR	1,199	14	85			
TOT	8,442	27				

All squares x 100

2. TMT Da 33/45, $\bar{X}$	378	386	398	405	424	434	429	407	Weight (mg)
BLK $D_1F_1, D_2F_2, \bar{X}$	391	397	397	413	409	424	451	412	
REP 2	385	391	397	409	417	429	440	410	

TMT	3,955	6	1,609	10.687	.001>P	***
BLK	122	1	122	0.812	.50>P>.25	NS
INT	1,058	6	176	1.171	.50>P>.25	NS
ERR	2,108	14	151			
TOT	12,944	27				

All squares x 100

3. TMT Da 33/43, $\bar{X}$	2.012	020	021	014	024	029	2.020	K_D-value
BLK $D_1F_1, D_2F_2, \bar{X}$	2.018	016	026	020	014	008	2.017	
REP 2	2.015	018	023	017	019	018	2.018	

TMT	159	5	31.7	0.354	P>.75 NS
BLK	48.2	1	48.2	0.538	.50>P>.25 NS
INT	593	5	119.	1.324	.50>P>.25 NS
ERR	1,075	12	89.6		
TOT	1,875	23			

(data-2) x 1000

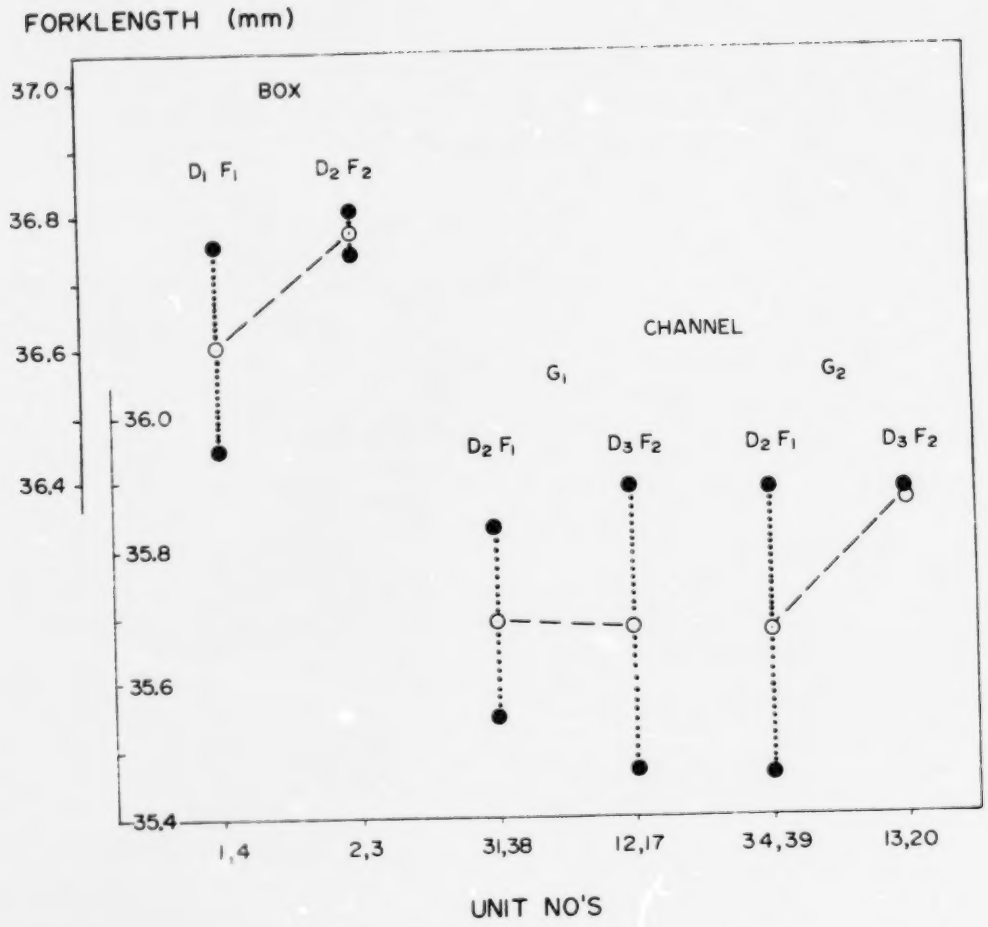

Fig. 6. Mean length of all samples of fry from box and channel units indicated, arranged by flow and gravel depth.

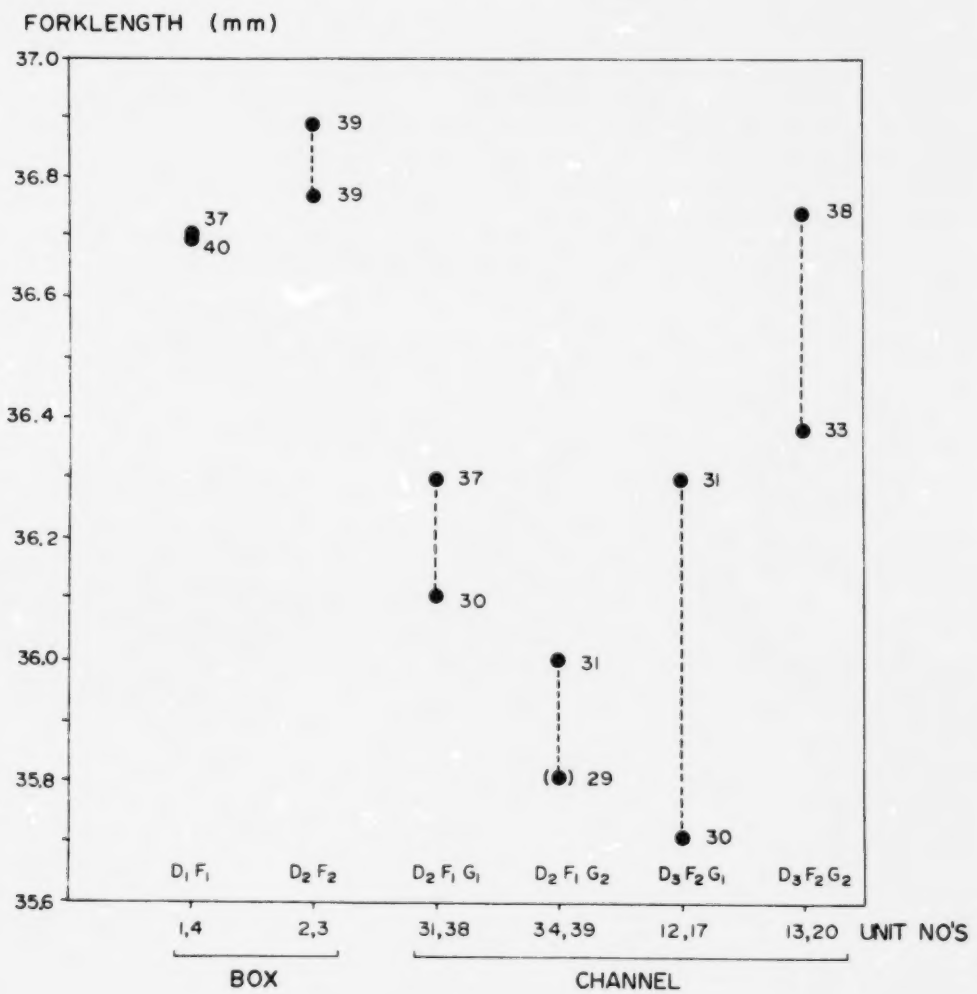

Fig. 7. Weighted (for daily abundance) mean lengths of fry from box and channel units shown, arranged by density, flow, and gravel depth. The median emergence day for each unit is given.

in lengths. Small differences existed among units and showed patterns similar to those observed among lengths, Table 12 and Fig. 8. For example, on fish from dates 15, and 22, 24, 27 combined, smallest mean weights occurred at high density, high flow, and shallow gravel (F_2 D_3 G_1), and the largest at low density, low flow, and shallow gravel (F_1 D_1 G_1). These results were quite similar to those obtained for lengths, Tables 6 and 9, and Figs. 3 and 4. The deep gravel (G_2) showed reduced weights at the alevin stage at both flow rates, but at the fry stage only at the low flow rate (F_1). Here, at the high flow rate (F_2) the deep gravel (G_2) fish were considerably heavier. Further, at the alevin stage the low flow (F_1) fish were considerably heavier than the high flow (F_2) ones; at the fry stage no clear difference emerged. Effects of density are consistent among all treatments: weights decrease with increasing densities ($D_{1,2,3}$). Analysis of variance, Table 13, showed only the density effect to be statistically significant, $.025>P>.01$.

Mean weights of fish from the sampler baskets decreased slightly but consistently with increasing flow rate and increasing fish density, but neither trend was significant by 2-way ANOVA, Table 8 (test 2), and Fig. 5.

Mean weights of fish from the deep-gravel boxes increased significantly ($P<.001$) with time due to growth during the 12-day period migrant samples were taken, but no consistent difference emerged associated with the two density and flow combinations used, Table 11, section 2.

ALEVIN AND FRY DEVELOPMENTAL INDICES

The developmental index, K_D, is a type of condition factor that, due to a gradually diminishing yolk reserve during larval development, is an accurate index of the stage of development (Bams 1970). Recent work by Heming (1981) supports the validity of this index for chinook alevins reared at four different temperatures. Its value is around 2.0 during final larval stages in all Oncorhynchus spp., and a common mean value on samples of wild migrant chum fry is around 1.96. At temperatures around 6°C its value decreases by about 0.004 daily (see, for example, Bams op. cit.). In alevin samples, taken on days 1 and 15, the values obtained reflect the population average; in fry samples (days 22 and later) the values are those of fish that had emerged only. The stage of development of the latter groups was, presumably, more advanced than those of the fish remaining.

During the alevin stage influence of density and flow was noted; both factors accelerated development at higher levels, Fig. 9 and Table 14. The flow effects were statistically significant by 2-way ANOVA, the density effects were not, Table 15. Increased gravel depth tended to accelerate development, particularly at the extremes of the available range of conditions.

Differences among treatments were greatly reduced during fry migration, as demonstrated by the samples from days 30 and 31. They were statistically not significant, as shown by ANOVA of certain groups of treatments (Fig. 9 and Table 16). Still, a noticeable trend remained for slower development at the lower flow (F_1), except in the high density, shallow

Table 12. Mean weights, in mg, of alevins and fry migrants from all channel units, from samples taken on day 15 and days 22, 24, 27 combined. Also given are treatment ranks, by date.

	Flow 1						Flow 2					
	G_1			G_2			G_1			G_2		
Density 1	(32)	379	405	(33)	379	398	(15)	367	392		-	
							(16)	380	400		-	
	(37)	390	404	(40)	369	395	(21)	379	414		-	
							(22)	379	401		-	
Ranks		10	10		3 1/2	6		5 1/2	8 1/2			
Density 2	(31)	378	404	(34)	371	391	(11)	376	387	(14)	369	407
	(38)	379	391	(39)	383	399	(18)	382	397	(19)	370	399
		7 1/2	6		5 1/2	3 1/2		7 1/2	2		2	8 1/2
Density 3	(35)	384	400		-		(12)	351	399	(13)	369	400
	(36)	384	395		-							
	(41)	378	386		-		(17)	362	380	(20)	377	395
	(42)	384	395		-							
		9	3 1/2					1	1		3 1/2	6

Unit numbers are in brackets.
Ranges: 357-385 = 371.0 $\pm$ 14.0 mg, 390-405 = 397.5 $\pm$ 7.5 mg.

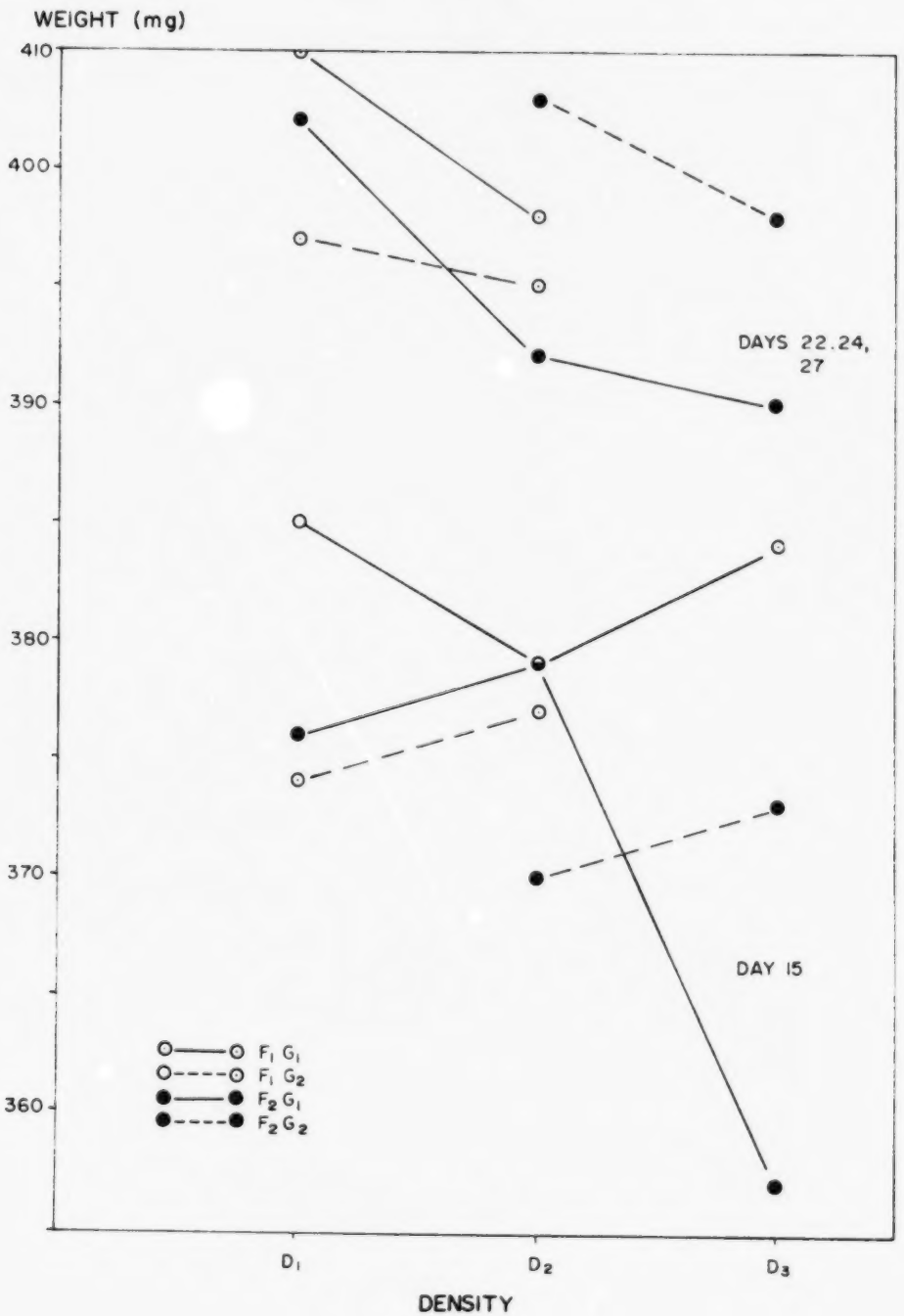

Fig. 8. Mean total wet weights of alevins and fry for all 10 treatment combinations, by density, on two dates.

Table 13. Mean fry weights, in mg, and ANOVA's on various treatments as indicated. Each datum is an average for 3 sampling dates (days 22, 24, 27) and 2 replicates. All squares are x 100.

1. TMT = $D_{1,2,3,\bar{X}}$ BLK = $F_{1,2,\bar{X}}$ REP = 6

					at G_1
	404.7	397.5	393.9	398.7	
	401.6	391.8	389.9	394.5	
	403.1	394.7	391.9	396.6	

	SS	df	MS	F	P	
TMT	8,259	2	4,130	5.121	.025>P>.01	*
BLK	1,598	1	1,598	1.982	.25>P>.10	NS
INT	107	2	53	0.066	P>.75	NS
ERR	24,193	30	806			
TOT	34,158	35				

2. TMT = $F_{1,2,\bar{X}}$ BLK = $G_{1,2,\bar{X}}$ REP = 6

				at D_2
397.5	391.8	394.7		
395.0	403.0	399.0		
396.3	397.4	396.8		

TMT	81.7	1	81.7	0.103	.75	NS
BLK	1,127	1	1,127	1.422	.25	NS
INT	2,802	1	2,802	3.537	.10>P>.05	+
ERR	15,843	20	792			
TOT	19,853	23				

Table 14. Mean developmental indices, K_D, of alevins and fry from all channel units on day 15 and days 30, 31. Also given are treatment ranks, by date.

	Flow 1						Flow 2					
	G_1			G_2			G_1			G_2		
Density 1	(32)	2.166	2.045	(33)	2.149	2.046	(15)	2.163	2.052		-	
							(16)	2.152	2.033		-	
	(37)	2.194	2.048	(40)	2.170	2.038	(21)	2.169	2.039		-	
							(22)	2.152	2.038		-	
Ranks		10	8		5 1/2	5		5 1/2	4		-	
Density 2	(31)	2.172	2.039	(34)	2.176	2.052	(11)	2.151	2.018	(14)	2.146	2.043
	(38)	2.178	2.055	(39)	2.163	2.050	(18)	2.135	2.040	(19)	2.143	2.035
		9	9		7 1/2	10		2	1		3	3
Density 3	(35)	2.170	2.038		-		(12)	2.144	2.047	(13)	2.136	2.040
	(36)	2.171	2.034		-							
	(41)	2.165	2.036		-		(17)	2.159	2.040	(20)	2.137	2.049
	(42)	2.175	2.032		-							
		7 1/2	2					4	6		1	7

Ranges, day 15: 2.137 to 2.180 = 2.159 $\pm$ .0215,

days 30, 31: 2.029 to 2.051 = 2.040 $\pm$ .0110.

Unit numbers are in brackets.

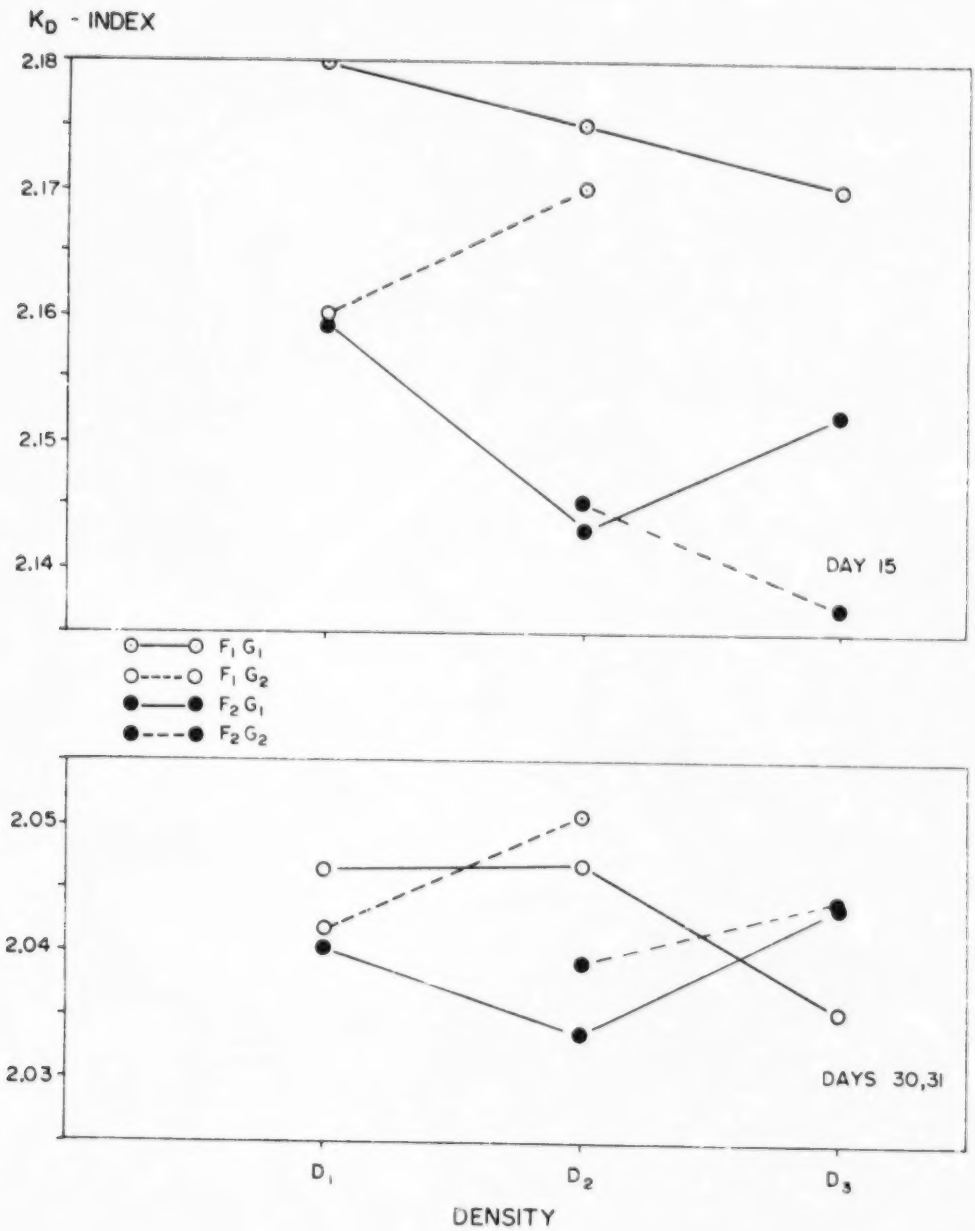

Fig. 9. Mean developmental indices (K_D) of alevins and fry for all 10 treatment combinations, on two dates, by density.

Table 15. Mean alevin developmental indices, K_D, and ANOVA's (squares x 10^5), on various treatments, on sampling day 15.

1. TMT = $D_{1,2,3,\bar{X}}$	2.180	2.175	2.171	2.175	at G_1
BLK = $F_{1,2,\bar{X}}$	2.159	2.143	2.152	2.151	
REP = 2	2.170	2.159	2.161	2.163	

	SS	df	MS	F		
TMT	249	2	124	1.132	.50>P>.25	NS
BLK	1,728	1	1,728	15.733	.01>P>.005	**
INT	98	2	49	0.446	.75>P>.5	NS
ERR	659	6	110			
TOT	2,734	11				

2. TMT = $F_{1,2,\bar{X}}$	2.175	2.143	2.159		at D_2
BLK = $G_{1,2,\bar{X}}$	2.170	2.145	2.157		
REP = 2	2.172	2.144	2.158		

TMT	1,625	1	1,625	27.651	.01>P>.005	**
BLK	8	1	8	0.136	.75>P>.50	NS
INT	25	1	25	0.417	.75>P>.50	NS
ERR	235	4	59			
TOT	1,892					

3. TMT = $D_{1,2,3,\bar{X}}$	2.149	2.140	2.158	2.149	at F_2
BLK = Up/down,$\bar{X}$	2.139	2.148	2.161	2.149	
REP = 2	2.144	2.144	2.159	2.149	

TMT	610	2	304	3.497	.10>P>.05	+
BLK	1	1	1	0.009	P>.75	NS
INT	163	2	81	0.931	.50>P>.25	NS
ERR	524	6	87			
TOT	1,297					

Table 16. Mean fry developmental indices, K_D, and ANOVA's on various treatments, on sampling dates 30, 31. (All squares x 10^5).

1.	TMT = $D_{1,2,3,\bar{X}}$	2.046	2.047	2.035	2.043	at G_1
	BLK = $F_{1,2,\bar{X}}$	2.040	2.029	2.044	2.037	
	REP = 4	2.043	2.038	2.039	2.040	

	SS	df	MS	F	P	
TMT	126	2	63	0.421	.75>P>.50	NS
BLK	176	1	176	1.174	.50>P>.25	NS
INT	704	2	352	2.349	.25>P>.10	NS
ERR	2,698	18	150			
TOT	3,704	23				

2.	TMT = $F_{1,2,\bar{X}}$	2.047	2.031	2.039		at D_2
	BLK = $G_{1,2,\bar{X}}$	2.051	2.039	2.045		
	REP = 4	2.049	2.035	2.042		

TMT	743	1	743	2.933	.25>P>.10	NS
BLK	138	1	138	0.545	.50>P>.25	NS
INT	18	1	18	0.071	P>.75	NS
ERR	3,038	12	253			
TOT	3,936	15				

3.	TMT = $D_{1,2,3,\bar{X}}$	2.042	2.018	2.047	2.036	at F_1
	BLK = Up/down,$\bar{X}$	2.038	2.040	2.040	2.039	
	REP = 2	2.040	2.029	2.044	2.037	

TMT	493	2	246	1.365	.50>P>.25	NS
BLK	40	1	40	0.223	P>.75	NS
INT	509	2	254	1.409	.50>P>.25	NS
ERR	1,083	6	181			
TOT	2,125	11				

gravel (D_3 G_1) treatment. In the deep gravel treatments (G_2) lower fish densities and increased flow tended towards advanced development in the migrant fry.

In the sampling baskets, stage of development was virtually the same at all three locations (EU's=0,7,14) in the high flow (F_2) channel and the first location (EU=0) in the low flow (F_1) channel (Fig. 5). However, the two locations further downstream in the low flow channel showed increasingly delayed development. Differences associated with flow and distance downstream were not significant by 2-way ANOVA, Table 8, test 3. However, in an orthogonal one-way comparison of the low (F_1) and the high (F_2) flow channels, at each of the three locations (EU = 0, 7, 14), we note, respectively,

$\bar{X}_1$=2.039, $\bar{X}_2$=2.040, F=0.015, df=1,6, P>.75; NS,
$\bar{X}_1$=2.042, $\bar{X}_2$=2.040, F=0.134, df=1,6, P>.50; NS, but
$\bar{X}_1$=2.056, $\bar{X}_2$=2.040, F=17.827, df=1,6 P<.01, **.

Clearly, at the low flow rate cumulative effects reduced the growth rate significantly at EU=14.

Developmental indices of the gravel box fry did not vary noticeably with time over most of the period of emergence, Table 11, section 3. There was a change on the final sampling day, date 45, when the average K_D-values far exceeded any seen previously (about 2.037), indicating the emergence of culls.

ENVIRONMENTAL FACTORS

Dissolved Oxygen (DO).

Values for intra-gravel DO-levels varied from near saturation to less than 50% saturation, depending on location in channel, flowrate, fish density, and stage of development (time), Table 17. Levels usually were between Davis' (1975) protection level "B" (76% saturation) and level "C" (57% saturation). As might be expected, the lowest values occurred in the low flow, deep gravel (F_1 G_2) units, where DO always was below level "C".

Determinations in the supra-gravel water layer were consistently higher than those along the bottom, Table 18. Expressed as a ratio, (DO within gravel/DO above gravel) x 100 in %, the following reductions in level were observed (first row of data points).

	High-flow channel		Low-flow channel	
Denominator DO	Single	6 cm	Single	6 cm layer
supra-gravel	86.9	62.3	81.3	54.3
outflow	88.8	63.9	90.3	59.8

Table 17. Intra-gravel oxygen, ammonia, and pH values, obtained from all keeper-channel and incubator units, at four successive weekly intervals.[a]

Unit[a]	Treatments[b]	Oxygen in (mg/L)				Un-Ionized Ammonia in (µg/L)				pH			
		March 11	March 18	March 25	April 1	March 11	March 18	March 25	April 1	March 11	March 18	March 25	April 1
11	F_2 D_2 G_1	9.24	8.59	9.59	8.15	0.000	0.024	0.000	0.024	7.01	7.06	7.12	7.07
13	F_2 D_3 G_2	7.32	5.23	7.18	4.30	0.106	0.140	0.140	0.222	6.93	6.97	7.02	6.88
15	F_2 D_1 G_1	9.24	9.54	9.59	9.31	0.008	0.039	0.050	0.041	7.00	7.06	7.10	7.06
17	F_2 D_3 G_1	8.84	8.28	7.91	8.73	0.056	0.105	0.109	0.086	6.99	7.01	7.04	7.01
19	F_2 D_2 G_2	7.03	6.57	6.32	5.58	0.114	0.164	0.148	0.177	6.89	6.94	6.97	6.92
21	F_2 D_1 G_1	8.47	9.05	9.39	8.84	0.054	0.065	0.061	0.086	6.94	7.05	7.07	7.02
12	F_2 D_3 G_1	8.09	6.99	8.00	9.55	0.106	0.139	0.039	0.055	6.94	6.97	7.03	7.06
14	F_2 D_2 G_2	6.93	6.20	6.49	6.51	0.127	0.164	0.183	0.178	6.89	6.95	6.94	6.90
16	F_2 D_1 G_1	9.24	6.34	9.45	9.48	0.007	0.042	0.056	0.045	7.03	7.09	7.11	7.04
18	F_2 D_2 G_1	8.18	7.92	9.39	8.89	0.088	0.049	0.074	0.077	6.98	7.02	7.09	7.04
20	F_2 D_3 G_2	6.78	5.92	5.96	4.69	0.172	0.199	0.236	0.234	6.93	6.91	6.97	6.84
22	F_2 D_1 G_1	9.05	9.05	9.06	8.74	0.020	0.065	0.083	0.075	7.01	7.04	7.07	7.04
31	F_1 D_2 G_1	9.53	8.59	9.47	7.76	0.004	0.035	0.057	0.051	6.98	7.06	7.09	7.06
33	F_1 D_1 G_2	7.80	7.37	6.59	4.04	0.111	0.163	0.217	0.204	6.97	6.98	6.97	6.91
35	F_1 D_3 G_1	6.45	8.28	8.83	7.86	0.030	0.047	0.115	0.115	6.83	7.02	7.06	7.00
37	F_1 D_1 G_1	6.07	6.45	8.10	8.10	0.045	0.113	0.120	0.109	6.98	6.97	7.02	6.99
39	F_1 D_2 G_2	7.22	4.47	7.25	4.69	0.134	0.162	0.174	0.221	6.96	6.90	7.00	6.86
41	F_1 D_3 G_1	8.28	7.52	7.31	7.18	0.113	0.145	0.155	0.161	6.98	6.95	7.00	6.92
32	F_1 D_1 G_1	8.47	8.21	9.98	8.53	0.030	0.064	0.047	0.035	7.02	7.04	7.09	7.06
34	F_1 D_2 G_2	7.51	5.80	5.73	4.17	0.173	0.170	0.268	0.189	6.94	6.92	6.93	6.88
36	F_1 D_3 G_1	8.57	7.35	8.66	-	0.039	0.086	0.089	0.114	7.03	7.03	7.06	7.00
38	F_1 D_2 G_1	5.39	8.78	8.17	8.32	0.049	0.066	0.095	0.094	7.00	7.03	7.02	6.98
40	F_1 D_1 G_2	4.62	4.41	5.63	4.41	0.181	0.182	0.234	0.220	6.94	6.95	6.93	6.92
42	F_1 D_3 G_1	8.18	7.83	6.69	6.21	0.100	0.142	0.114	0.179	6.97	6.98	6.96	6.88

Table 17. (cont'd)

Unit[a]	Treatments[a]	Oxygen in (mg/L) March 11	Oxygen in (mg/L) March 18	Oxygen in (mg/L) March 25	Oxygen in (mg/L) April 1	Un-Ionized Ammonia in (µg/L) March 11	Un-Ionized Ammonia in (µg/L) March 18	Un-Ionized Ammonia in (µg/L) March 25	Un-Ionized Ammonia in (µg/L) April 1	pH March 11	pH March 18	pH March 25	pH April 1
Inflow													
-all units		10.59	10.50	10.77	10.78	0.000	0.000	0.000	0.000	7.07	7.07	7.18	7.15
Outflow													
-channel I_a		10.01	9.81	9.65	9.35	0.004	0.040	0.111	0.106	7.05	7.07	7.09	7.12
-channel I_b		9.92	10.00	9.62	9.20	0.008	0.045	0.056	0.110	7.05	7.07	7.10	7.10
-channel II_a		9.24	9.12	8.70	8.12	0.017	0.090	0.129	0.146	7.04	7.04	7.04	7.03
-channel II_b		9.63	8.89	8.47	8.27	0.016	0.088	0.120	0.122	7.01	7.04	7.06	7.03
Boxes													
01	F_1 D_1	9.0	9.3	9.0	9.4	0.040	0.053	0.176	0.174	7.10	7.00	7.09	7.08
02	F_2 D_2	9.5	9.4	9.0	9.2	0.000	0.046	0.103	0.113	7.03	6.99	7.02	7.01
03	F_2 D_2	9.2	9.3	9.0	9.0	0.008	0.041	0.094	0.145	7.03	6.98	7.05	6.98
04	F_1 D_1	9.1	9.0	8.9	9.2	0.056	0.070	0.081	0.136	6.98	6.96	7.06	6.99

[a]Temperatures of the incoming water on the four dates were, respectively, 7.8, 7.9, 8.2, and 8.0 °C.
[b]Unit and treatment codes are explained on Table 1.

Table 18. Supra-gravel oxygen, ammonia, and pH values, obtained from all six units in one half of each of the keeper-channels, on two sampling days, 2 wk apart.

Unit[a]	Treatments	Oxygen (in mg/L)		Un-Ionized Ammonia (in µg/L)		pH	
		March 13	March 27	March 13	March 27	March 13	March 27
12	F_2 D_3 G_1	10.11	10.17	0.000	0.028	7.09	7.10
14	F_2 D_2 G_2	10.01	10.34	0.000	0.032	7.10	7.10
16	F_2 D_1 G_1	10.01	10.08	0.000	0.037	7.12	7.10
18	F_2 D_2 G_1	10.40	9.90	0.000	0.050	7.11	7.09
20	F_2 D_3 G_2	9.82	9.68	0.014	0.057	7.06	7.07
22	F_2 D_1 G_1	9.72	9.32	0.005	0.061	7.08	7.05
32	F_1 D_1 G_1	10.58	-	0.000	0.017	7.14	7.09
34	F_1 D_2 G_2	10.21	10.19	0.000	0.033	7.15	7.09
36	F_1 D_3 G_1	10.06	9.68	0.016	0.068	7.12	7.06
38	F_1 D_2 G_1	9.72	9.31	0.023	0.082	7.07	7.05
40	F_1 D_1 G_2	9.63	8.83	0.035	0.094	7.09	7.04
42	F_1 D_3 G_1	9.24	8.86	0.064	0.104	7.06	7.01
Inflow -both channels		10.59	10.75	0.000	0.008	7.14	7.13
Outflow -channel I_b		9.63	9.39	0.018	0.079	7.06	7.09
Outflow -channel II_b		9.44	8.15	0.044	0.146	7.08	7.04

[a]Unit and treatment codes are explained on Table 1.

The effect increased markedly with increasing gravel depth and decreasing flow rate. Similarly, DO of the outflow-water was consistently higher than that measured in the gravel of the unit immediately upstream (second row of data points in above table). The differentials with outflow were influenced similarly by gravel depth but somewhat less by flowrate. These data support a common contention: conditions in the gravel can be more extreme than those in the water layer above and in the effluent flow. Meaningful DO determinations, therefore, must be obtained from inter-gravel waters. DO-levels in the deep-gravel incubator outflows always exceeded 75% saturation.

Un-ionied ammonia levels reached a maximum value of 0.27 µg/L at pH=6.93, which is below the critical level as defined in "Summary of water quality criteria for Salmonid hatcheries", Sigma Resource Consultants, 1979. Levels increased proportionally, although not linearly, with fish density and reduction in flow rate, Tables 17 and 18. No influence was indicated associated with gravel depth.

pH-levels decreased proportionally with fish density and reduction in flow rate. The lowest sample value was 6.83.

Nitrite concentrations usually were undetectable and were always less than 10 µg/L.

DISCUSSION

Owing to the complexity of the material to be covered in this discussion, it may prove helpful to consider the results of this study separately on two levels of interest: that of the hatchery operator, and that of the biologist. The former would be interested mostly in effects large enough to significantly affect operational efficiency, or fish survival in the hatchery or following release. Such large effects would make changes desirable in prescribed culture parameters such as fish density or flow rate. The biologist's interests would center on biological processes that affect and are affected by operational aspects of the technique under study. Small differences that may not be of operational significance may contribute substantially towards understanding of the animal and expand the scope of incubational techniques in general.

OPERATIONAL CONSIDERATIONS

To deal with the practical aspects first, let us consider the responses obtained to the various treatments, arranged by environmental (operational) factor.

1. Gravel depth

The major division here is between the deep-gravel, upwelling incubation-box technique and the Japanese-style incubation channel. Excluding the unnecessary mortality that occurred among eggs on hatching screens in the low flow channel at the highest density, all survivals to the fry stage were equally high, generally over 95%, and totally satisfactory. The mortality on the screens undoubtedly could be prevented by installation of a second screen to reduce the depth of eggs on each screen to no more than two layers, thus ensuring adequate gas exchange for all eggs.

Swim-up began on average a week earlier in the channels than in the boxes. This was not due to acceleration of the developmental rate, which was mostly the same in comparable units, but to swim-up behavior being initiated at an earlier stage. Depth of gravel was most closely associated with age at swim-up: the shallow-gravel treatment resulted in the earliest emergence, the 6-cm depth was significantly later, at least at the higher flow rate, and the deep-gravel (box) treatment was the latest of all at both flow rates. Because production channels impose no restrictions on outmigration, migration would take place even earlier there than in the experimental units.

Fish size at emergence was associated with gravel depth primarily through time of emergence: earlier emergence leads to smaller size. In addition, small differences could be attributed directly to some treatment factors. Gravel depth alone could suppress or promote growth, depending on other environmental factors present at the same time. In general, deeper gravel certainly increased fish size, but only if the water exchange (particularly the linear velocity?) was sufficiently high. In the channel, at normal flow rates and loading densities (our F_1, D_2) greater than normal (single layer) gravel depth was decidedly disadvantageous, presumably related to the significantly reduced dissolved oxygen levels observed there.

2. Flow rate

Flow rate was associated with mortality only at the egg stage, when excessive depth (more than 2 layers) of eggs on the hatching screens resulted in significant mortality at the low but not at the high flow rate. As suggested earlier, addition of a second screen to reduce the depth of eggs should eliminate the problem.

Emergence rates increased somewhat with increased flow, especially at the higher densities. Generally, this effect was marginal.

The higher flow rate generally favoured fish size, as would be expected on the basis of improved gas exchange. Complications arise, however, through interactions with gravel depth and fish density, affecting metabolite exchange as well as fish behaviour. The combination high flow, high density, and shallow gravel depth, for example, led to "clumping", the phenomenon of alevins migrating up or downstream and piling up, many layers deep, at either end of the available space. The excessive energy expenditure and the, presumably, locally poor environmental conditions led to greatly reduced size among these alevins. The phenomenon was of relatively little consequence in the small, mutually separated units of the experiment, but in a larger (production) scale unit consequences of high density would likely be serious.

Reducing the water velocity by increasing the water depth should alleviate the undesirable condition without affecting the necessarily high flow volumes required for high-density rearing.

3. Fish density

Two aspects of fish density must be considered: (1) the in situ density, i.e. the number of fish per unit of area in an experimental unit (referred to as $D_{1,2,3}$ in this study), and (2) the cumulative density, i.e. the number of fish upstream of a given point in the channel (referred to as egg-units, $EU_{0,7,14}$). As demonstrated, both kinds act upon the fish through differences in concentration of various metabolites. Additionally, in situ density may also act more directly, by such means as degree of filling of intersticial spaces and behavioral stimulation through increased number of contacts.

Neither aspect of density had any effect on survival to the fry stage. Therefore, at least within the limited length of the channels and the environmental factors as imposed, no critical combination was reached the fry could not handle. Reductions in growth and developmental rates were observed, however, which demonstrated that conditions were far from optimal in certain units or locations. Also, dissolved oxygen determinations within the gravel of the units situated furthest downstream demonstrated that even in the shallow gravel oxygen content was reduced to as little as 58% of that of the incoming water. To "scale up" from an experiment such as this, therefore, requires caution; it should be done gradually while evaluating certain key parameters, such as oxygen.

Emergence was generally delayed with increasing density, but only for about one day near the mid-point of the runs. Differences in density were of lesser influence than those in gravel depths.

Size of fish was affected relatively little by in-situ densities. Among alevins a slight acceleration of growth rate (lower K_D) was evident with inceasing density, but this was not reflected in an increase in length. There was a trend for reduced size (both length and weight) at increased density among migrant fry from the shallow gravel units. Average differences were small and negligible for practical purposes.

Cumulative density effects were more pronounced. Emergence from any upstream unit was, on average, about 20% faster at mid-run than from its replicate situated 7.0 EU's further downstream. There were no significant differences in length between these paired groups of fry. However, among the fish incubated in the sampler baskets the effects of increasing EU's on size were larger and statistically significant. Reductions in size (both length and weight) were greatest in the low-flow channel, but even these were only 1 1/2% of their mean, a difference equivalent to less than 2 days' growth in the channel. A response of this magnitude may not be of practical importance; however, when scaling up beyond the maximum EU=14 used in this experiment (equivalent to 92,000 fish/40 lpm), the effect undoubtedly will become more pronounced and may well become harmful to the fish. Caution is advised.

BIOLOGICAL CONSIDERATONS

To gain insight into the underlying biological processes requires interrelating the various observed responses. Interpretation is difficult owing to interaction and confoundment. Factors nor responses can be understood in isolation. For example, to understand why a difference in fish size and/or time of emergence has occurred requires knowledge of the stage of development of the groups involved; only then can we distinguish between two perhaps equally likely but fundamentally quite different causes: a change in yolk conversion efficiency, or one in developmental rate. To know the difference is to understand how a particular technique affects the animal and, hence, what its limitations and possibilities might be.

1. Survival

Egg to fry survivals were high in all experimental units. Eggs on hatching screens in the channels experienced difficulty only when placed in layers more than 2 eggs deep at the low water velocity (approx. 33 cm/min). Ignoring this one preventable exception, egg-incubation parameters were fully satisfactory throughout the ranges presented.

Alevin survival was also entirely satisfactory in all units, with most survivals well above 95%. Two units had less, between 93 and 94%, both at the high density (D). Assuming this small difference to be real, it could indicate the beginning of reduced survival. Alternatively, it may have been caused by the fish that had escaped from the high density units, as described earlier, by pushing through the divider screens. Survivals in the sampler baskets were all over 95%.

The general conclusion is that environmental conditions were satisfactory in all boxes and channels, even at the downstream end of the low flow channel (at EU=14), in terms of survival to the fry stage. Survivals over 90% are obtained routinely in Japanese production hatcheries (Moberly and Lium 1977), in various trials with deep-substrate incubators (Bams and Simpson 1977), and in keeper-channels at Thornton Creek when hatching screens were used (Bailey 1979).

2. Time of emergence

There were significant differences in time of emergence among treatments. The clearest relationship was with gravel depth, the general effect being for emergence to become later as gravel depth increases. For example, the average coded median emergence dates were, for the shallow-gravel, high-flow (F G) units, about 11; the 6-cm gravel, high-flow (F G) units, 16; and the deep-gravel boxes, 20; also see Fig. 2. However, in the low flow channel emergence decreased little with increasing gravel depth (Fig. 2), indicating that a reduction of flow in the gravel not necessarily induces the fish to migrate later. Comparison of age and stage of maturity at time of migration must be deferred until the stage-of-development data have been discussed.

Time of emergence was influenced by an uncontrolled factor, most likely associated with locomotory activity of the fish. For example, the influence of in-situ fish density sometimes was the opposite of what one might expect on the basis of increased levels of metabolites. Mean proportions of fish emerging during the first migratory period decreased with increasing density levels in the low flow channel (Fig. 2; and Table 4, comparison 1) and in the fast flow channel during the second period (Table 3). Similarly, increased flow rates tended to increase migration rates, especially in the shallow gravel treatments (Table 3), in spite of metabolite levels being more favourable. Even though these differences were small and statistically not significant, they are still important because they go against expectations and thus may be indicators of previously not recognized events or processes.

A consistent pattern emerges if we assume levels of locomotory activity to vary directly with changes in density and flow rate. This contention also agrees with the observed "clumping" and passage through dividing screens only at high levels of density and flow rate, differences in general activity and patterns of activity observed occasionally in the units, and earlier experimental work on sockeye alevins (Bams 1969), which demonstrated increased levels of alevin activity associated with increased levels of fish density and CO_2 dissolved in the supply water. If behaviour is the responsible factor, different kinds of activity must be involved because density-related activity reduced egress, perhaps by fish tending to move actively upstream (rheotaxis), whereas increased flow rate increased egress, possibly through current-assisted displacement downstream. Such events would decrease, respectively increase, the density of fish near the outlet port and thus affect the rate of egress from the unit. Even though these ramblings may well be in error, there is no doubt about alevin behaviour being of possibly crucial importance to the performance of incubational devices and of the need to pay attention to it when unexpected results occur.

The influence of cumulative density (EU's) on time of emergence emerges clearly from the comparison of treatment pairs (replicates) which, by design, always were three experimental units and 7 EU's apart. Such pairs showed consistent differences during both migratory periods. The proportions of fish emerged from the downstream units reduced by 11.5 to 18.0%, mean 15.0%, in the four groups calculated (t-tests on p. 11). Presumably, as the downstream effects accumulate over longer distances in production-length channels, the associated reduction in average migration rate may become quite large and result in an increasingly more protracted period of outmigration for the entire channel. This delayed emergence contrasts sharply with emergence patterns in upwelling deep-substrate incubators, which routinely show vary rapid rates of egress, e.g. greater than 15% per day for the middle half of all box runs in this experiment, as opposed to 3 to 5% for most channel units.

3. Length and weight

Differences in fish size were observed in response to most experimental factors. None of these differences exceeded the equivalent of from 5 to 10 days' growth at the prevailing temperatures. Based on alevin and migrant fry lengths it was demonstrated that

1. increased gravel depth had a major effect, deleterious at low (F_1) but beneficial at high water velocity (F_2);

2. at normal gravel depth (G_1) and density (D_2), there was an advantage in doubling the flow rate (to F_2), similar in effect to reducing the density to half-normal (D_1) at the same water velocity;

3. at the highest density (D_3) there was no advantage in increased flow at normal gravel depth (G_1);

4. the cumulative density effect (EU's) was negligible.

The effect of cumulative density on length was significant, however, in fish incubated in the sampler baskets, at EU's of 0, 7, 14. This was most pronounced in the low flow channel, where both ends of the range showed more extreme values than were obtained elsewhere. I conclude that the high flow initially was a disadvantage, perhaps again by means of behavioral interference, but the higher velocity, or volume, soon became an asset in terms of population growth, presumably mediated through improved metabolite levels.

Superior size at emergence was demonstrated in all gravel-box groups when compared with the appropriate channel units, Fig. 6. However, large differences in emergence timing preclude a conclusion of superior growth. Stages of development must be taken into account simultaneously.

Differences in weight usually paralleled those in length. Exceptions were primarily associated with deep gravel and low flow treatments. Because differences in length and weight were associated with differences in stage of development, further discussion is postponed to the next section.

4. Stage of development and rates of development and growth

Stage of development of larval salmonids is conveniently expressed by the K_D-index (Bams, 1970). If samples of larval fish of the same initial population, absolute age, and temperature history have different mean K_D-values, the average rate of development experienced by each of these samples has been different, in proportion to the differences in K_D-value. Rate of development is primarily controlled by temperature (Gray, 1928[b]; Embody 1934), but is reduced by limiting, sub-standard environmental conditions (Brannon 1965; Shumway et al. 1964; Silver et al. 1963). Size obtained at any stage of development is controlled by the amount of yolk originally available and the growth rate experienced during development, (Gray 1928[a]). The two processes are essentially independent so that large or small fish may result from similarly sized eggs, at the same stage of development, depending on how efficiently the yolk was converted. Less than optimal environmental conditions during larval development, which may include periods of excessive locomotion, require expenditure of energy and thus reduce yolk available for growth and depress the instantaneous growth rate (Bams 1969). By comparing sample lengths and K_D-values together, we can distinguish between treatment effects arrived at by two different pathways, i.e. by a change in growth rate or in rate of development.

During the alevin stage rate of development generally accelerated with increasing density, flow, and gravel depth. This is deduced from decreasing mean developmental indices, Fig. 9 and Tables 14 to 16. The largest response occurred with increase in flow: at all densities and both gravel depths substantial decreases in K_D were evident. However, these increased rates of development did not all translate into increased rates of growth. Significant differences in yolk-conversion efficiency were already in evidence at day 15, i.e. the 39th day of the alevin period. Most notable is the lack of growth in the high density, high flow, shallow gravel (D_3 F_2 G_1) treatment. Both lower density treatments at this flow showed far superior growth, as did both available densities at the greater gravel depth. A small penalty in growth was exerted by the greater gravel depth, but the high density on the shallow gravel was of far greater influence. As noted before, the cause for this discrepancy may lie in the behavior of the animal: the shallow gravel likely provided insufficient cover in the presence of the faster flow to prevent extensive movement. This activity resulted in discontinuous distribution ("clumping") and high activity-related metabolic demand. In the deep-gravel treatments a much increased rate of development at the higher flow did correlate with increased size, but not quite to the same extent as observed in the fish on the shallow gravel. Obviously, there was a penalty in growth rate (yolk conversion efficiency) associated with the deeper gravel at both flow rates.

The second largest response in developmental rates was to gravel depth. A large change occurred at the low flow rate and the lowest density (D_1 F_1). Here a much accelerated rate of development was observed in the deep gravel (G_2) which did not, however, correspond with an increase in size. Why development only would accelerate under these conditions is difficult to imagine and I offer no explanation. At the high flow rate in the deep gravel (F_2G_2) an increase in developmental rate was associated with increased density and did correspond with an increase in size. Under these conditions behavioral influences apparently did not detract from the potential gain, and thus gave rise to a very large difference in size, Figs. 3 and 4.

The response to density per se, although never large, clearly was to accelerate developmental rate and increase size. Effects were modified by other factors, e.g. changes were generally minor at the low flow rate but much more pronounced at high flow, in both gravel depths. Why increasing density would accelerate development under certain conditions is not understood. It runs counter to effects expected with accumulation of metabolites in the micro environment, such as reduced developmental and growth rates demonstrated with the sampler basket fry. It has, however, been noted by fish-culturists and I have observed it repeatedly in various experimental situations.

The captive fry populations, reared in the sampler baskets and sampled simultaneously, demonstrated significantly different rates of development and growth at different locations in the channels, Fig. 5 and Table 8. Rates of development were identical in the upstream location of the low flow channel and in the three successive locations along the fast flow channel. However, fish size gradually decreased, i.e. growth rates steadily declined, in the order given. Evidently, in these four locations local conditions, which included the different flow rates, extracted an increasing net penalty in yolk utilization efficiency only, resulting in declining sizes at the same stage of development.

The situation was more complex in the slow flow channel. Here, conditions started out more favourable than in the faster flow channel. This was demonstrated by the sampler fish achieving superior growth while developing at the same rate. Going downstream, conditions deteriorated more rapidly here than in the fast flow channel, so that both lengths and weights decreased sharply while developmental rate slowed down as well. If the fish at the locations further along the channel were given the opportunity to develop further (longer) and bring their K_D-index down to the common value displayed by all the others, further growth would take place. Lengths would increase sufficiently to achieve about the same slope as that shown by the fish reared in the high flow, Fig. 5, right half. Weights too would increase a little and the end result would be two groups of two lines with similar slopes but lying some distance apart, i.e. showing different efficiency throughout. These results clearly demonstrate an interesting difficulty associated with high flow rates: if unnecessary, increased flow is stressful and will reduce growth. Of course, when metabolite levels in the environment are sub-optimal, increasing the flow rate may well be beneficial.

Stage of development and size data obtained on emerged fry are affected by selective migration: fry do not migrate from the gravel at a stage of development average to the total population, but, at least early in the migration, at more mature stages of development (Bams, unpublished data). Differences in mean (population) size associated with rate of development may thus be reduced in such fry samples. Despite this, migrant fry demonstrated notable differences in size and stage of development according to treatment.

Results are essentially the same as observed with the alevins, but differences have become attenuated (Fig. 8, top versus bottom range). Fish from the high flow treatments are still significantly advanced, at both gravel depths, relative to fish from the low flow, only less so. Fry from the deep-gravel treatments have become less advanced and now overlap with those from the corresponding shallow-gravel treatments. Fish from the highest density treatment slowed down more than any others and now coincide with the corresponding shallow-gravel group. A greatly reduced variability in characteristics is noted among all treatments at this stage. This may, at least in part, derive from the advancing development of the fish, which renders them increasingly independent of ambient conditions and enables them to avoid unfavourable micro-habitats.

Lengths obtained at the fry stage, Fig. 4, and to some extent weights, Fig. 8, demonstrate that in the deep-gravel treatments the high flow induced accelerated development and promoted growth. At the low flow, development and especially growth were depressed compared with all other treatments. As with the alevins, increasing fish density in the deep-gravel treatments resulted in markedly increased yolk-conversion efficiency: the fish were already larger at less advanced stages of development, Fig. 4 and Fig. 9. In the deep gravel, therefore, high flow is of great advantage and high fish densities further enhance growth, despite reduced oxygen levels (Table 17). Thus, some of the best overall performance was observed in deep gravel, at the high flow, and the highest density ($D_3F_2G_2$). Deep gravel is not necessarily always desirable, however; poorest overall performance also occurred in the deep gravel, but at low flow and lowest density ($D_1F_1G_2$).

In the shallow gravel the higher flow generally accelerated development. However, only at the middle density (D_2) did this result in some enhanced growth as well, so that yolk conversion efficiency, generally, was reduced at the higher flow. Contrary to what was observed in the deep gravel, increased density consistently decreased fish size here, marginally in lengths but markedly so in weights. Because lengths decreased proportionally less than weights, yolk conversion efficiency was inversely related to fish density in the shallow-gravel treatments. Best performance here occurred at the lowest density and the low flow ($D_1F_1G_1$). This relationship contrasts with that observed in the deep-gravel treatments, where reductions in weight were similar but led to markedly increased lengths at less advanced stages of development (Figs. 8, 4, 9). This unexpected phenomenon has no likely explanation at the moment. Its discovery would be of obvious importance to our understanding of gravel incubation.

In terms of fry quality, the deep-gravel incubators produced fry superior to those from the Japanese-style hatchery. Since most of the differences were associated with differences in time of emergence, channel fry that emerged late and those resulting from treatment combinations that promoted early swim-up least (e.g. high flow and deep gravel) tended to resemble the box fry most. Differences in fry quality criteria, expressed as treatment averages, were established in the following characteristics.

Yolk-conversion efficiency was highest in the gravel boxes and decreased in the channel units, mostly in association with decreasing gravel depth.

Size at emergence of box fry exceeded that of fish from all channel treatments. Differences in length were significant but small, generally less than 5%.

Stage of development at emergence was closer to that observed in natural runs in the box fry than in the channel fry. Average degree of immaturity of channel fry compared to box fry was the equivalent of about 7 days of development at prevailing temperatures. However, sample mean values varied considerably among different treatments and in time during each group's period of emergence.

Time of emergence was closely tied to stage of development and was significantly later in box-fry than in channel-fry groups. Deep-substrate incubated fry are known generally to emerge prematurely by about a week to 10 days compared to naturally produced runs (Bams 1970; Bailey et al. 1975; Bams and Simpson 1977). The channel fry emerged an additional 4 to 7 days earlier than the box fry and were quite immature in appearance, often with yolk material still showing externally. Rate of emergence was much faster in the boxes than in the channels.

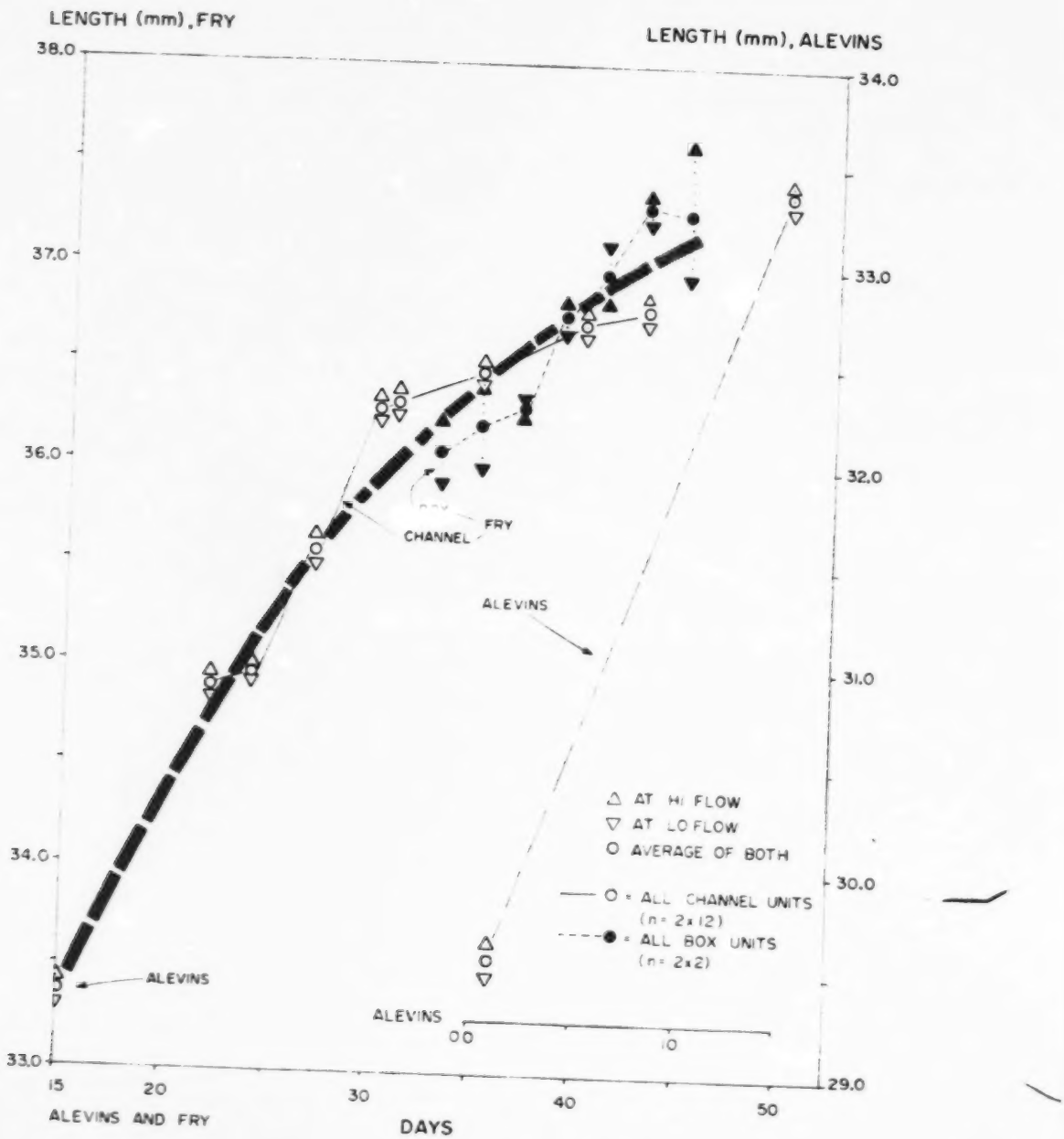

Fig. 10. Mean lengths of alevins and fry for all 10 treatments and the controls, by sampling day. Separate values for high and low flows and their average are given.

SUMMARY OF RESPONSES BY FACTOR

1. Gravel

In the channels, developmental rate of alevins tended to increase with greater gravel depth, but interactions with flow and density complicated the associated changes in growth rate: some increased and some decreased. Shallow gravel promoted early emergence, especially at the high flow rate. At any time, deep-gravel fish lagged marginally in stage of development. This corresponded with a somewhat smaller size in these fish in the low flow treatments, but in the faster flow treatments they were larger, indicating superior yolk conversion efficiency under that combination of factors.

In the deep-gravel boxes, yolk conversion was the most efficient of all treatments. Box fry emerged at significantly larger average sizes, but at significantly later mean dates than the channel fry.

2. Flow

Greater flow generally favored faster development, more strongly so in alevins than in migrant fry. This resulted in generally somewhat larger sizes as well. At the migrant-fry stage this effect had become very small and inconsistent among the shallow-gravel treatments, but it was still pronounced among the deep gravel ones. Comparison of mean lengths for all channel units combined showed, for each of 7 sampling days, a larger mean size of fish from the high flow, Fig. 10, triangular symbols. Time of emergence generally accelerated with the higher flow in the shallow gravel treatments, but it decelerated in the deeper gravel.

3. In-situ density

Increasing the density over the limited range tested, tended to accelerate the rate of development of alevins and fry in the shallow-gravel (G_1) treatments. This did not, however, result in increased size generally and, hence, efficiency of yolk conversion decreased with increasing density. In the deep-gravel (G_2) treatments developmental rates generally decreased with increasing density, but lengths increased. In this curious case, therefore, yolk conversion efficiency markedly improved with increasing density.

Swim-up was generally delayed by increasing density, marginally in the deep gravel but more strongly so in the shallow-gravel treatments. There were two notable exceptions to this pattern: at the low flow, fish of the highest density emerged much earlier than expected, whereas at the fast flow fish of the lowest density migrated much later.

4. Cumulative density (EU's)

Lengths and weights of the captive sampler populations decreased proportionately along the high flow channel, while developmental stages

remained the same. Hence, yolk-conversion efficiency was, but developmental rates were not, correlated with metabolite levels present at high flow. In the low-flow channel the developmental rate did drop with increasing EU-levels, together with greatly changing lengths and weights. Adjusting (by calculation) the stages of development to those observed in the high-flow channel, showed higher yolk-conversion efficiency at all 3 locations in the slow-flow channel. Relative efficiency decreased with increasing EU-levels, similar to that observed in the fast-flow channel. These changes parallel the gradients established for DO, un-ionised ammonia, as well as pH.

The same general conclusions derive from comparing the spatially separated replicates of all treatments. However, these results were far less precise, presumably because of greater ranges in micro-environmental conditions in the sections than in the cages. An additional response shown by fish of these treatment pairs was a significant delay in time of emergence at the higher EU levels.

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